VOLUME LXI NUMBER 6

THE

BOTANICAL GAZETTE

*JUNE 1916*

# REDUCTION DIVISIONS IN THE POLLEN MOTHER CELLS OF ALLIUM TRICOCCUM

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 215

MILDRED NOTHNAGEL

(WITH PLATES XXVIII–XXX AND ONE FIGURE)

## Introduction

In accordance with a suggestion of Dr. D. M. MOTTIER made while the author was attending Indiana University during the summer of 1914, material showing the reduction divisions of *Allium tricoccum* was examined with the idea of comparing it with the results of a previous investigation of *Allium cernuum* (**24**). In many stages the results were the same, but a further investigation of other phases of the spore mother cell development has forced the author to change some views previously held.

The nuclei are large and the haploid number of chromosomes is only 8; consequently, individual members or portions of the spirem can be traced through various stages with less difficulty than is usually encountered.

Literature shows a great diversity of opinion as to whether or not the chromosomes visibly retain their individuality throughout the resting period; also concerning the structure of the resting nucleus; the state of the chromatin as it enters the synaptic ball; the actual time and method of reduction; and the origin of the spindle fibers. These questions the author has attempted to answer.

## Material and methods

The material was collected along the steep, damp, shady banks of Clear Creek, 6 miles south of Bloomington, Indiana. Collections were made 4 days and 5 days apart, from June 30 to July 27, and while some of the anthers at the earlier date failed to show differentiation of sporogenous tissue, many from the later collections were in the shedding conditions. Often all stages from resting to tetrad would be found in a single umbel.

Strong chromo-acetic acid was used for killing and fixing, and allowed to act 36 hours, the fluid being changed once or twice during that period, after which the material was washed 18–24 hours by means of repeated changes of water, slowly dehydrated, cleared in chloroform, and then imbedded in 52° paraffin.

Sections were cut 5–12 $\mu$ thick, varying with the stages sought. For the spindle and in some instances for the spirem, Flemming's modified triple stain was found to be preferable, although for all other phases, especially the early prophases, Haidenhain's iron-alum-haematoxylin gave the best results, lichtgrün in clove oil occasionally being used for a counter-stain.

## Description

### PRESYNAPTIC AND SYNAPTIC STAGES

An attempt to determine the structure of the resting nucleus and the origin of the various stages that follow by first studying that resting condition would be difficult and indefinite. The investigation must begin with a stage concerning which there is little dispute, and from this may be traced the subsequent steps. Such a condition is to be found at late telophase of the last division in the sporogenous tissue, even though the chromosomes are more or less united by anastomoses, caused by considerable enlargement of the nucleus which followed the close association at early telophase (fig. 1). While still retaining this distinct individuality, although united with one another by anastomoses and at the same time slowly approximating end to end, a series of vacuoles appear along the median longitudinal portion of each chromosome (figs. 1–4), this being first made apparent by chromatin staining fainter

along that portion (figs. 2, 3). In the beginning the vacuoles are short, narrow slits (figs. 2, 3), but later, owing to their enlargement,

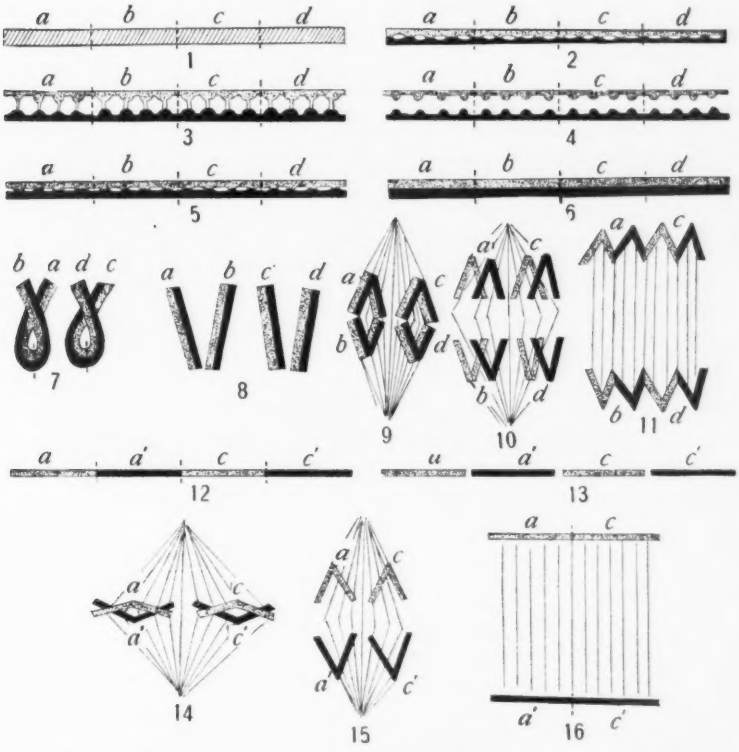



FIG. 1.—Diagram to illustrate reduction divisions as found in *Allium tricoccum*, 4 chromosomes only being shown: (1) telophase of last division of sporogenous tissue; (2) late telophase of same; (3) resting nucleus of pollen mother cell; (4) late resting condition; (5) going into synapsis; (6) condition of thread during synapsis and spirem; (7) segmented; (8) condition at time of third contraction and multipolar spindle; (9) metaphase; (10) anaphase; (11) telophase; (12) spirem of daughter nucleus; (13) segmented spirem of daughter nucleus; (14) metaphase; (15) anaphase; (16) tetrad or granddaughter nucleus.

the chromatin bordering the two sides of the vacuoles becomes more widely separated, although still joined together by portions or strands of chromatin that separate the vacuoles, resulting in

each chromosome having a ladder-like appearance (figs. 2–8). The rate of vacuolization is by no means uniform, as will be seen from an examination of figs. 2–5, and the distribution of chromatin over the ladder thread is very uneven, being heavier at the junction of the sides and the connecting strands. During this process several nucleoli appear in the comparatively large open spaces of the nucleus, each large nucleolus containing a relatively large oblong vacuole (figs. 5, 8).

It must be kept in mind that the ladder structures with their two sides and connecting strands have arisen from single somatic chromosomes, and are the result of a series of vacuoles along their median longitudinal axis. The so-called typical resting stage consists entirely of these structures, therefore, still joined more or less with one another by the anastomoses that arose at the last telophase (figs. 5–8). In the very early prophase the sides of the ladder are very fine (figs. 3, 4), but as the chromatin material increases, the threads become heavier and more uniform (figs. 5–8), while at the same time the anastomoses break down, and the connecting strands of chromatin between the two parallel sides grow finer and finer (figs. 7, 8) until they entirely disappear, leaving as a result two parallel threads (fig. 8), which are daughter halves of single somatic chromosomes.

As the parallel spirems, now entering synapsis, contract and condense, they gradually approach each other and approximate, at times twisting about one another (fig. 9) and resulting in a single thick spirem (figs. 10–13) which is the condition of complete synapsis, the heavy thread appearing as a homogeneous structure twisted and coiled about itself (figs. 11, 12), causing the mass to have a lumpy, granular appearance (fig. 12). At no time during this period, when sectioning and staining have been the best, is the thread lost to view (figs. 9–14); for even at the time of the greatest contraction, portions of the thread may be traced across the mass (fig. 11). This step in development is not necessarily uniform, for portions of the spirem in synapsis have been observed showing the double nature distinctly (fig. 10).

While these activities are going on, the nuclear cavity as well as the entire cell enlarges; although most of the growth is after the

chromatin material has contracted considerably. As the result of measuring many nuclei, only those being measured in which the entire nucleus was contained in the one section, the following statement may be made safely. Since the diameter of the contracted mass is considerably less than that of the nucleus just previous to contraction, or of the resting nucleus (figs. 7–12), synapsis is a true contraction. The synaptic mass lies almost or entirely against one side of the nuclear cavity, with the nucleolus just outside or partially held by a few strands of the spirem.

### FORMATION OF BIVALENTS

As the synaptic mass loosens up, a comparatively thick, smooth thread may be seen twisting and winding about; and gradually loops free themselves, extending for various distances into the cavity (figs. 13, 14). It was stated that "a comparatively thick, smooth thread" was freed from the mass; while in fact the thread is irregular in outline and stains irregularly, the darker places being those denser chromatin aggregations seen in the ladder-like structure of the resting nucleus (figs. 3–9).

The spirem, although double in nature, is composed of single somatic chromosomes placed end to end, the double nature having arisen by the vacuolization or splitting of single chromosomes during late telophase of the last division of the sporogenous tissue.

When the spirem is entirely disentangled, loops of varying lengths are at first irregularly distributed within the nucleus (fig. 15); later, when they are peripherally arranged, the loops are longer and may be traced even entirely around the cavity, forming what is known as the hollow spirem (fig. 16). The double nature is rarely discernible during this latter period, since the thread has condensed and grown until it appears as a homogeneous structure staining uniformly throughout. Occasionally the halves of the thread separate (fig. 16) and may be seen even to twist about each other, the origin being in early synapsis (fig. 9, left side).

At the close of the hollow spirem stage the thread thickens and becomes entangled in the center (fig. 17), continuing until the typical second contraction results; which phase consists of the well known radiating loops that usually extend to the periphery

(fig. 18). The loops represent somatic chromosomes end to end which separate at the outer bend; that is, at the curve away from the entangled mass (figs. 19, 20, 21) rather than at the lower bend. Each radiating loop, therefore, does not represent the bivalents as seen in figs. 21*x*, *y*, 22. Instead, one arm of a loop pairs with and twists about an arm of a neighboring loop, this being plainly evident in the material. Fig. 19 illustrates such a condition, for here *a* and *a'* were formerly a continuous loop, likewise *b* and *b'*; but, following separation, *a* and *b* twist about one another, then opposite ends in all probability form a loop, resulting in *a*+*b* forming a bivalent, as seen in figs. 21*x*, *y*, 22, 23.

The bivalents of the aggregation continue to crowd together until only paired free ends extending from a dense mass can be recognized (fig. 20). When these segments loosen up, the chromosomes are found to be growing shorter and thicker. In case a misunderstanding should arise concerning the transition from fig. 21 to fig. 22, separate chromosomes have been drawn (figs. 21*x*, 21*y*). After the bivalents become dissociated and well distributed, eight are readily counted, each one representing 2 somatic chromosomes that formerly were end to end, although now they are twisted about each other. At times the 2 members of the bivalent are still continuous, that is, forming a loop; while in other cases they are not, causing the bivalent to be open at both ends. In either case it is not due to the splitting or to a separation of the halves of the spirem thread, since that spirem thread is composed of 16 somatic chromosomes with an end to end arrangement.

### FROM THIRD CONTRACTION TO DAUGHTER NUCLEUS

About the time the bivalents are more or less distributed within the nuclear cavity, the fibers, which stain blue with Flemming's triple stain, appear outside the nuclear membrane (figs. 22, 23), running parallel to it, the ends extending out into the cytoplasm into which they merge (figs. 23, 24). While these are increasing in number and the nuclear membrane is disappearing, a peculiar behavior of the chromosomes has been noticed which seems to have a definite relationship to phases in the development of the spindle. The nuclear membrane slowly and unevenly disappears (fig. 23),

this being accompanied by further growth of fibers. These fibers gradually appear within the nuclear space even before the membrane is entirely gone (fig. 24). When this activity first begins, the chromosomes move slowly toward the center, so that by the time of the stage shown in fig. 25, where the membrane has entirely disappeared, the bivalents are tightly massed in the center, forming a *third contraction*. Step by step the kinoplasmic fibers encroach upon the chromosomes (figs. 25, 26), until they come in contact with them (fig. 27), this being immediately followed by the loosening up of the aggregation (figs. 28, 29). By this time there is a strong multipolar complex, which is apparent as early as the disappearance of the membrane. The number of poles may be many and irregularly arranged (figs. 28–31), and as the fibers are rearranged into sharper points, the chromosomes become more and more dissociated (figs. 28–31) and scattered upon the fibers. Those bivalents which formerly consisted of the two end to end somatic chromosomes and formed a loop (fig. 22) have separated transversely, making 16 chromosomes or 8 pairs (figs. 29, 30, 30*x*). Fastened to each member of a pair, approximately at the middle, is a group of kinoplasmic fibers (fig. 30*x*) extending to one of the several poles. As the multipolar spindle changes to the bipolar shape, the chromosomes that formerly were scattered irregularly upon the fibers (figs. 29–32) gradually arrange themselves upon the spindle's equator (figs. 32–35). During this latter period the chromosomes shorten considerably, having reached their largest size during multipolar phase, as well as slowly untwisting.

The forms that the pairs may assume now are various; some remaining slightly twisted, others form a U, while still others may become linked with one another, forming an X, or the ends of the pair may remain in contact, forming a ring. No form was found to be conspicuously dominant (fig. 31). Polar views of the spindle first show the chromosomes not to be peripherally placed (fig. 32), although before metaphase is completed they take that position (fig. 33). At this time the chromosome count again can be taken without difficulty.

The individual fibers that are attached to each chromosome may become so closely associated at the point of union with them

that the collection at first sight appears as a homogeneous mass and a part of the chromosome (fig. 34). These wefts retain their individuality for their full length and many times terminate in a very blunt pole (fig. 34).

During metakinesis, that is, just at the time when the paired segments separate, the dissociation of the two approximated halves, which originated in the resting stage (figs. 1–11), is finally completed (fig. 35), showing that the splitting or vacuolization of the somatic chromosomes in early prophase was in preparation for the homotypic division. There are now 16 chromosomes, for each half becomes entirely separated from its partner and does not again approximate (figs. 36–39). As the 16 members approach the poles, they shorten considerably, and as they crowd together an end to end formation results, thus forming an irregular spirem 16 chromosomes in length (figs. 37, 38). The crowding together continues until the entire chromatin mass is so closely associated that it is very difficult to distinguish the individual members; although, after the new nuclear membrane is formed, the looping spirem is again easily recognizable (fig. 39).

### HOMOTYPIC MITOSIS

After the new membrane has been formed and the chromatin mass loosened up (fig. 39), anastomoses between portions of the looping spirem are everywhere evident. A coarse reticulum is formed as a result of the continual growth of the nucleus and the chromatin (fig. 40); but a resting stage is never reached. The spirem, which consists of 16 segments arranged end to end, will come directly from this reticulum (figs. 41, 42). This continuous spirem is quite regular in outline at first (fig. 41), but as the time for segmentation and formation of the multipolar complex approaches, the thread is more irregular and the outlines of the segments evident (figs. 42, 43); although it is not until the bipolar spindle is visible that the spirem separates into the 16 chromosomes (fig. 44). Simultaneous with this separation there is a pairing; so that 8 pairs of chromosomes come to lie upon the spindle fibers (figs. 44, 45). The paired chromosomes do not take the characteristic forms of the heterotypic mitosis, for at this time, although

there is a pairing, there is no twisting about of the members; but, instead, the tendency is to assume more elongated forms, such as hooks, rods, or wide U's. One member of each pair passes to a pole, where again there is an end to end approximation, as in heterotypic mitosis, of the 8 chromosomes or the haploid number (fig. 49). The tetrad, or 4 granddaughter nuclei, each containing 8 chromosomes, may all lie in one plane, although at times they occupy two planes.

## Discussion

### PRESYNAPTIC AND SYNAPTIC STAGES

Since the investigation began with the examination of the late telophase of the last division of the sporogenous tissue while the individual chromosomes were still plainly evident, although joined together by anastomoses, it is clear to the author that there is not a pairing of somatic chromosomes in fig. 1, or that a previous approximation has taken place. If such were the case, 8 chromatin groups only would be visible. Even at this early phase the vacuoles are making their appearance along the median longitudinal line. The chromatin bordering these vacuoles could not be called linin, although the later enlargement of these forms the fine chromatin structure (figs. 2–8) that ALLEN (**1**), MOTTIER (**21, 22, 23**), STRASBURGER (**30, 31**), DIGBY (**7**), and others term linin. Furthermore, the heavier masses of chromatin granules are due to the nature of vacuole formation; for, as they enlarge, a greater amount of chromatin will be left at the angles between the vacuoles, thus giving rise to the so-called "chromomeres" strung along at irregular intervals on a linin thread.

BEER (**2**), MOTTIER (**22, 23**), and MOTTIER and NOTHNAGEL (**24**) find a single spirem formed from the network, in which condition it enters synapsis; while ALLEN (**1**), GRÉGOIRE (**16**), GRÉGOIRE and WYGAERT (**17**), BERGH (**3, 4**), YAMANOUCHI (**32, 33**), ROSENBERG (**27**), and OVERTON (**25, 26**) see a pairing of spirems either previous to or during synapsis, this act involving the pairing of somatic chromosomes, presumably maternal and paternal, after which they approximate and at metaphase of heterotypic mitosis separate. Nothing more than an inference or a suggestion has

been found in the literature showing that the double nature of the spirem of the heterotypic mitosis is due to the splitting or vacuolization of somatic chromosomes in the early prophase. In a paper on *Galtonia* by Miss DIGBY (**7**), the split for the division at metaphase of the somatic mitosis is shown to arise by the vacuolization in early prophase, thereby forming the split or the double thread. A similar condition is found in *Vicia Faba* by SHARP (**28**), and by FRASER and SNELL (**12**). As the result of the conditions found, Miss DIGBY says: "By taking a broad and comparative view of this heterotypic prophase in relation to the somatic prophase, one is forced to admit that the parallelism of the one is homologous with that of the other"; although in her conclusion she states that "the parallel portions in both represent longitudinal halves of somatic chromosomes, and are probably sister halves of the same chromosome, which are now severally coming together and condensing to form the somatic or univalent chromosome." The series of drawings are incomplete at this critical period, and any conclusion would have to be based upon her drawings 39*a* and *b*, and 40, none of which is later than the writer's figs. 3 and 5. Furthermore, steps illustrating the origin of these figures from figs. 30 and 31 have not been shown, and the gradual transition from the "beaded" resting nucleus (DIGBY **7**, figs. 33, 36, 37) to the double condition of the spirem after synapsis appears to be more of a theory or an inference than a statement of observed facts.

In the early prophases of the heterotypic mitosis of *Vicia Faba*, Miss FRASER (**11**) finds conditions corresponding to those observed in *Allium tricoccum*. In this paper she describes diamond-shaped meshes that are due to the splitting of the somatic chromosomes in the early prophases; then later, that is, in synapsis, the cross-connections between the meshes breaking down, thus forming the spirem; and finally, in early anaphase, each chromosome splitting preparatory to homotypic mitosis, the origin of the split having been seen in the diamond meshes. The idea is very similar to that described by the author, but as in the paper by Miss DIGBY (**7**), Miss FRASER fails to have a series sufficiently close to demonstrate the origin of the split and the formation of the spirem from these

meshes. While the resting nucleus is said to consist of diamond-shaped meshes, it is in all probability the same as the ladder-like formation of *Allium tricoccum*.

As has been previously stated, the number of chromosomes in *Allium tricoccum* is small and the size large, so that the difficulty so often encountered in following the development is considerably lessened. Throughout these critical phases every precaution has been taken to prevent overlooking important stages. Since the pollen mother cells at the upper end of a loculus are a little earlier than those at the lower end in development, at least two consecutive stages could be found in a single section. In every case the later of the two stages observed has been found in the upper end of the loculus, where the third has been found and drawn, decreasing to a great extent the possibility of omitting critical stages or placing the wrong interpretation upon the origin of the double character found in the resting nucleus. Had figs. 5, 7, or 8 been the first nuclei observed after the telophase of the previous division, the conclusion could readily be drawn that the double thread arose by the pairing of somatic chromosomes; but, after seeing the beginning of vacuolization (figs. 1, 2) and following its development step by step (figs. 2–9), no other conclusion is possible than that the paired threads going into synapsis are the two halves of single somatic chromosomes, and not paired somatic chromosomes, as held by GRÉGOIRE (**16**) and YAMANOUCHI (**32, 33**).

Fig. 8 illustrates the breaking down of the connecting strands between the two sides of the ladder-like structures, and on the right side of this figure the act has been completed, leaving the halves completely separated except for the portion connecting them at the end. MOTTIER (**22**) states that "the delicate threads joining the chromatic masses may be found lying close to each other and parallel, but this does not signify that a double spirem is in process of formation"; although in his figures of this stage (MOTTIER **22**, figs. 1, 17, 34) he shows nuclei very similar to that in fig. 5 of *Allium tricoccum;* and by tracing this further it is very probable that the origin of the double nature of the hollow spirem, as described by MOTTIER (**21, 22, 23**), might be found.

No suggestion of the spiral arrangement with the strands radiating from a "Chromatinknoten" as described by BØNNEVIE (5) has been observed.

That the chromosomes retain their individuality and do not break up into a network is claimed by GRÉGOIRE (15), YAMANOUCHI (32, 33), SHARP (28), OVERTON (25, 26), STOUT (29), BONNEVIE (5), and LAWSON (19); this is also evident in *Allium tricoccum*. Although the chromosomes become considerably vacuolate and thus cause the net appearance, the individual members never lose their entire individuality, as can be seen from the description and drawings, and later, owing to a larger amount of chromatin material and a more even distribution of it, the chromosomes form a more or less continuous thread, the spirem.

Little growth occurs during the later stages of the resting nucleus, but when the chromatin mass starts to contract, it increases slightly in size, but not to the extent claimed by LAWSON (19); that is, that the appearance of the contracted mass is due to the growing away of the nuclear membrane. Comparison of figs. 8, 9, 10, and 11[1] will make this clear, as fig. 11 is a drawing of an entire nucleus, the dimensions of the chromatin mass being considerably less than that of figs. 7 or 8. It is not until the mass has contracted extensively that the large increase in size of the nuclear cavity occurs (figs. 10, 11). Were it but an apparent contraction, as LAWSON (18) states, due to the inflow of karyolymph into the nuclear cavity, the osmotic pressure would be decreased, not increased, and the increase in size would be the result of the larger amount of fluid that it must hold.

As synapsis approaches, the two halves of the spirem gradually approximate (figs. 9, 10, 11), the final step usually being accomplished during synapsis (fig. 11); although even as late as the stage shown in fig. 10 the act might not have been completed along the entire length. This process corresponds to that described by GRÉGOIRE (14, 15), YAMANOUCHI (32, 33), OVERTON (25, 26), and ALLEN (1), although these investigators claim it

[1] Figs. 1–12 were made with a magnification of 3500, while fig. 12 has a magnification of 2650, so that comparison of the latter with the former is not to be made where questions of size are concerned.

to be the approximation of whole somatic chromosomes, or pseudo-reduction.

FORMATION OF BIVALENTS

With close observation during early spirem, the double nature is still discernible, although it is rare that the two halves separate as found in *Allium cernuum* (MOTTIER and NOTHNAGEL **24**), and as commonly found in *Lilium*. The lumpy condition of the thread at this time is due to the larger chromatin collections of the early prophase (figs. 5–9), this appearance being the basis of the statements of FARMER and MOORE (**9**), MOTTIER (**22**), and others who interpret such as dividing chromomeres, thereby initiating the longitudinal split. This dual nature has been seen in most cases, although it has been attributed to two sources. Those believing in pseudo-reduction in early prophase assert that it is the two spirems that have paired, while MOTTIER (**21, 22, 23**), STRASBURGER (**30, 31**), BEER (**2**), GATES (**13**), FARMER and MOORE (**9**), and FARMER and SHOVE (**10**) say that the spirem has split in preparation for the homotypic division. In this latter case, however, the split was not traced to its origin. The two halves soon approximate so closely that the spirem appears as a homogeneous structure (figs. 15, 16). Comparatively few ends are seen when sections are cut 12 $\mu$ thick, and from all of those observed it appeared to be due to cutting. So far as the stages to follow are concerned, it would make little or no difference whether the spirem be continuous or non-continuous.

At first, as formerly stated, the spirem is irregularly placed within the nuclear cavity (figs. 14, 15), this being followed by a peripheral arrangement, thereby forming the typical hollow spirem as described by MOTTIER (**21, 22**), MOTTIER and NOTHNAGEL (**24**), and BEER (**2**); at which time the thread may be followed for a considerable distance. As it thickens and shortens, the second contraction period is entered upon, although OVERTON (**26**) fails to find such a stage in *Thalictrum purpurascens*, *Calycanthus floridus*, and *Richardia africana;* also GRÉGOIRE (**16**) fails to observe it at times in *Lilium speciosum;* both regarding such an act as of little significance in the reduction division. The author believes this step to be of considerable importance.

Up to and including the second contraction, a nucleolus is usually present (figs. 17, 18), although some of the drawings fail to show such, as it was either not included in that section, or it was purposely left out, owing to obscuring too great a portion of the other chromatin material.

During second contraction (fig. 8), the characteristic radiating loops extend from the tangled mass, the first sign of segmentation being seen at the peripheral end of the loop, resulting in the free ends being next to the nuclear membrane (figs. 19, 20). ALLEN (1) has reported a similar observation in *Lilium canadense*, but this is contrary to the reports of MOTTIER (**21, 22, 23**) and BEER (**2**), these investigators describing the radiating loop as forming the bivalent. With the loop segmenting at its outer bend, it necessarily follows that either the bivalent is continuous at the lower end, as stated in the description of this stage, or that segmentation occurs at both ends, followed by a pairing of single somatic chromosomes. During the period of segmentation and formation of bivalents, the chromatin thread contracts, although not suddenly (cf. figs. 18–24), resulting in 8 thick bivalents being fairly evenly distributed within the nuclear cavity.

All cytologists agree upon the point that in heterotypic mitosis a bivalent consists of 2 somatic chromosomes, but concerning the mode of formation there is a great difference of opinion. ALLEN (1), BERGH (**3, 4**), GRÉGOIRE (**16**), GRÉGOIRE and WYGAERT (**17**), OVERTON (**25, 26**), ROSENBERG (**27**), and YAMANOUCHI (**32, 33**), who claim there is a pairing of somatic chromosomes or spirems in early prophase, state that the bivalent is composed of 2 segments that in the spirem were side by side, reduction therefore occurring by the pairing of 2 spirems; while BEER (**2**), FARMER and MOORE (**9**), FARMER and SHOVE (**10**), and MOTTIER (**21, 22, 23**) demonstrate that it is formed by the twisting about of 2 somatic chromosomes that previously were end to end in the spirem, thus causing a transverse segmentation to be responsible for the reduction. *Allium tricoccum* confirms this latter view, and if the series here given be followed, it will be seen that the arms *b* and *a* of fig. 19 have not arisen from the separation of 2 approximated spirems of a previous stage (fig. 18), yet doubtless these 2 will

by a gradual thickening (figs. 20, 21, 21*x*, *y*, 22) form a bivalent (fig. 22).

Each bivalent, therefore, is composed of 2 somatic chromosomes, presumably maternal and paternal, that previously had an end to end arrangement in the spirem, and which may be open either at both ends or at one end. In the latter case a later segmentation will separate the two. So far as any result that is to follow is concerned, the author conceives it to be of little importance whether it be the one condition or the other. Some claim that the bivalents are always open at both ends, which would necessarily be the case were they derived from a paired spirem; but definite cases have been found where the bivalents were continuous at one end (figs. 22, 23), and in fig. 22, lying under another bivalent, will be seen one in which the two arms have not twisted about each other as yet, but are lying more or less stretched out in the cavity. Under such circumstances the bivalent could not have been formed as GRÉGOIRE (**16**), ALLEN (**1**), and YAMANOUCHI (**32, 33**) have claimed.

To repeat once more, each arm of a bivalent is necessarily of a double nature, owing to the approximation of the two halves of single somatic chromosomes in synapsis, so that in cross-section a bivalent has a tetrad arrangement.

### FORMATION OF SPINDLE AND DAUGHTER NUCLEI

Nothing has been found in the literature describing the third contraction or its relationship to spindle formation.

LAWSON (**18, 20**) finds the weft of fibers, these being transformed cytoplasm, outside the nuclear membrane as early as the spirem stage, although in *Allium tricoccum* they are not visible until segmentation.

After carefully studying the paper entitled "Nuclear osmosis as a factor in mitosis" by LAWSON (**20**), and then comparing the same with results found in *Allium tricoccum*, many points of disagreement were encountered. As has been pointed out by FARMER (**8**), LAWSON has used the term "permeable membrane" in describing the nuclear membrane, after which he continues to speak of osmotic systems and exosmosis. In this discussion, when speaking of the membrane in this connection, the term "semipermeable

membrane" will be used. Undoubtedly the nuclear membrane, which is the inner limiting layer of the cytoplasm formed there by the contact of cytoplasm and karyolymph, is a semipermeable membrane, and also, at the time of spindle formation, exosmosis is taking place, since the nuclear cavity is gradually decreasing in size (figs. 22–27) from the time of development shown in figs. 22 and 23, when the fibers are first evident outside the membrane. Since the membrane results from the contact of cytoplasm and karyolymph, the same chemical reaction would occur when the nuclear sap gradually diffuses into the cytoplasm. Such is the author's interpretation of the weft of fibers outside the nucleus. The diffusion is gradual, and the precipitation would then be slight, resulting in the fine fibers. The cytoplasm is not forced to occupy more cubical space, as LAWSON claims, for karyolymph is steadily, though slowly, passing through this semipermeable membrane, and owing to the precipitation the fibers occupy the space left by the receding nucleus.

It is while the foregoing is occurring that the third contraction or massing of the chromosomes in the center of the cavity becomes so conspicuous (figs. 23–27), although as yet the fibers are not in contact with them; and furthermore, the membrane disappears previous to the filling up of the cavity by the fibers (figs. 24–26). If the plasma membrane completely invested the bivalents, as claimed by LAWSON, a cavity would be left between it and the fibers in the case of *Allium tricoccum* (figs. 25, 26), under which circumstances the fibers could not be moored to the membrane (LAWSON **20**).

It was owing to the contact of the two chemically different substances that the heavy plasma membrane was precipitated, but with the kinoplasmic fibers now being formed between the membrane and the reticulate cytoplasm, this chemical antithesis is decreased, resulting in a decrease in the amount of precipitation. In other words, the membrane becomes thinner and thinner until it either disappears entirely or becomes a part of the spindle fibers. When the nuclear cavity is completely filled with the kinoplasmic threads, the chromosomes loosen up, probably owing to the completion of exosmosis from the cavity, as well as partially on account of the osmotic systems within each chromosome.

The bivalents are now open at both ends and not quite as large as formerly, decreasing from now on (fig. 24). When they first loosen up, fibers are not fastened to each chromosome apparently; but as the multipolar complex forms, a weft becomes moored to each one, in many instances so conspicuous (figs. 29–35) that it appears to be homogeneous structure at the point of attachment, owing to the thick fibers and also to their close association.

Each chromosome, as stated by LAWSON (**20**), is saturated with karyolymph and is an osmotic system; although this does not necessarily mean that the old membrane must surround each member in order to accomplish this. If such were the case, the membrane would have to break up into the proper number of pieces, wrap about each chromosome, and then become sealed; a process which is far more complex than ever before attributed to a nucleus. Each chromosome will have the power to develop its own membrane, owing to diffusion of the sap from it, and since each then will have the same osmotic power as the nucleus did as a whole, the same process will continue as it did with the nucleus, resulting in the formation of a weft of fibers from each individual. The fact that these wefts are distinct from the other fibers points strongly toward this idea.

LAWSON'S theory that the shift from multipolar spindle to bipolar spindle is an expression of "lines of tensions" appears to the author to have little or no foundation, since the reticulate cytoplasm is not forced to occupy less cubical space than formerly.

The paired chromosomes, which formerly were tightly twisted about each other, gradually come to lie upon the equatorial plate; the fibers formed outside the nuclear membrane extending from pole to pole and the individual tufts of fibers attached to the chromosomes extending to but one pole. At metaphase the separation of whole somatic chromosomes, that previously were end to end in the spirem, is completed, this reduction being immediately followed by the longitudinal separation of the halves (fig. 35) of each of these, the origin of which was seen in the resting nucleus (figs. 2–10). Those believing in the pairing of somatic chromosomes or spirems in early prophase or pseudo-reduction have little to say concerning the origin of this split; while those claiming that

the spirem is a single structure splitting during the spirem stage demonstrate that the separation during anaphase is the result of this former activity.

Contrary to most reports, the halves of the chromosomes in *Allium tricoccum* become entirely dissociated during anaphase, so that a polar view of such shows 16 individuals, or the $2x$ number. These 16 remain distinct from now on, and at late anaphase or early telophase they join up end to end (fig. 38), after which the looping spirem becomes very much crowded. As some karyolymph still remains, this diffuses out and the nuclear membrane is formed about the densely crowded chromatin mass, as described by LAWSON (**20**) and YAMANOUCHI (**32**).

### HOMOTYPIC MITOSIS

A spirem consisting of 16 segments, that approximated end to end at late anaphase of the previous mitosis (fig. 38), forms early in the daughter nucleus (fig. 42), since a resting condition does not intervene. In all reports read concerning the homotypic divisions, the spirem is interpreted as being $x$ chromosomes in length and double, owing to the longitudinal separation during the previous anaphase. As the multipolar spindle appears, the spirem forms 16 segments (fig. 44) which immediately pair (fig. 45), forming 8 pairs of half chromosomes. It is probably owing to the rapidity of the pairing that previous investigators have claimed the longitudinal split to be completed at this time instead of during the heterotypic mitosis. Unless a close series had been followed and the end to end approximation of the half chromosomes been observed, the author would probably have made a similar interpretation. If each chromosome is to maintain its individuality, no other results could be expected.

All this goes to show that at metaphase of heterotypic division there is a reduction or separation of characters, but it is not until homotypic division that the reduction in number is actually accomplished.

## Conclusion

In comparing the nuclei during the reduction division, as seen in *Allium tricoccum*, with the nuclei during somatic division, as described by SHARP (**28**) for *Vicia Faba* root tips, it is seen that

both have a similar structure during the early prophase. The first difference is evident when, apparently owing to some osmotic force, the thread contracts into the synaptic ball. During this contraction there is an increase in chromatin substance, preparatory to the two rapid divisions which follow. At the time of second contraction, this condition undoubtedly being due to osmotic activity again, bivalents are formed. Following the third contraction, where it has been pointed out plainly that exosmosis is the factor underlying spindle formation and massing of bivalents, the members of each pair separate for opposite poles. Seemingly this last contraction, or the 3 contractions taken together, hold in check the dissociation of the halves, which in somatic mitosis would have occurred at this time; for immediately following the separation of whole chromosomes, the halves move apart, join end to end, and, as soon as a new spindle is formed, go to opposite poles.

From this investigation it appears to the author that on account of these various contractions, a regular somatic mitosis, although started normally, is first varied and then checked for a time, resulting in the heterotypic division, and not until homotypic division is the typical mitosis completed.

## Summary

1. During late telophase of the last division of the sporogeneous tissue a row of vacuoles appears along the median longitudinal axis of each chromosome, these enlarging until each member is a ladder-like structure. Accompanying this there is an end to end approximation. Such is the condition of the resting nucleus.

2. The paired threads entering synapsis and there approximating are the two sides of the ladder, the connecting strands having broken down. This process does not represent the pairing of two spirems. Throughout this period the chromosomes have retained their individuality.

3. The spirem, which consists of 16 end to end chromosomes, will take the form of radiating loops during second contraction, segmentation occurring at the outer bend. Each of the bivalents so formed consists of two somatic chromosomes that were end to end in the spirem.

4. Spindle fibers are the result of exosmosis of karyolymph into the cytoplasm, these being formed after the same fashion as the nuclear membrane. The membrane, if it persists, will be a part of the fibers.

5. The third contraction which accompanies fiber formation consists of a balling up of the chromosomes previous to the complete filling up of the cavity with fibers.

6. Each chromosome is an osmotic system in itself and capable of forming its own weft of fibers after the sap from the nuclear cavity has been exhausted.

7. The heterotypic division or the reduction of characters results from a transverse separation of whole chromosomes.

8. During early anaphase the halves of the chromosomes, which originated in presynapsis, separate longitudinally and at early telophase approximate end to end, forming the looping spirem of the daughter nucleus, $2x$ chromosomes in length. Division in homotypic mitosis, therefore, results originally from a longitudinal separation.

9. The transverse separation of the 16 segments during early metaphase of the homotypic mitosis is immediately followed by their pairing.

10. To all appearances a typical mitosis is begun, but is varied and delayed for a time by a heterotypic mitosis as the result of the various contractions, being finally completed in the homotypic division.

To Dr. J. M. COULTER and Dr. C. J. CHAMBERLAIN I wish to express my appreciation for their most helpful suggestions and criticisms during the progress of this work, and also to Dr. D. M. MOTTIER of Indiana University, under whom this work was commenced.

UNIVERSITY OF CHICAGO

## LITERATURE CITED

1. ALLEN, C. E., Nuclear division in pollen mother cells of *Lilium canadense*. Ann. Botany **29**:189–258. *pls. 6–9.* 1905.

2. BEER, R., Studies in spore development. II. On structure and division of the nucleus in the Compositae. Ann. Botany **26**:705–726. 1912.

3. BERGH, JULES, La formation des chromosomes hétérotypiques dans la sporogénèse végétale. II. Depuis la sporogonie jusqu'au spirème definitif dans la microsporogénèse de *l'Allium fistulosum*. La Cellule **21**: 383–397. 1904.

4. ———, La formation des chromosomes hétérotypiques dans la sporogénèse végétale. III. La microsporogénèse de *Convallaria majalis*. La Cellule **22**:41–53. 1904.

5. BONNEVIE, K., Chromosomenstudien. III. Chromatinreifung in *Allium Cepa* (?). Arch. Zellforschung **6**:190–253. 1911.

6. DAVIS, B. M., Cytological studies on *Oenothera*. II. Reduction division of *Oenothera biennis*. Ann. Botany **24**:631–653. 1910.

7. DIGBY, L., The somatic, premeiotic, and meiotic nuclear division of *Galtonia candicans*. Ann. Botany **24**:727–758. 1910.

8. FARMER, J. B., Nuclear osmosis and meiosis. New Phytol. **12**:22–28. 1913.

9. FARMER, J. B., and MOORE, J. E. S., The meiotic phase in animals and plants. Quart. Jour. Micr. Sci. **48**:489–555. 1905.

10. FARMER, J. B., and SHOVE, DOROTHY, On the structure and development of the somatic and heterotypic chromosomes of *Tradescantia virginica*. Quart. Jour. Micr. Sci. **48**:559–571. 1905.

11. FRASER, H. C. I., The behavior of the chromatin in the meiotic divisions of *Vicia Faba*. Ann. Botany **28**:633–643. 1914.

12. FRASER, H. C. I., and SNELL, F., The vegetative division of *Vicia Faba*. Ann. Botany **25**:845–855. 1911.

13. GATES, R. R., A study of reduction in *Oenothera rubrinervis*. BOT. GAZ. **46**:1–35. 1908.

14. GRÉGOIRE, V., Les résultats acquirés sur les cinèses des maturation dans les deux règnes. Premier mémoire Revue critique de la littérature. La Cellule **22**:221–376. 1905.

15. ———, Les fondements cytologiques des théories courantes sur l'hérédité Mendelienne. Ann. Soc. Roy. Zool. et Malacol. Belgique **42**:267–320. 1907.

16. ———, La formation des gémini hétérotypique dans les végétaux. La Cellule **24**:369–420. 1907.

17. GRÉGOIRE, V., and WYGAERT, A., La reconstruction du noyau et la formation des chromosomes dans les cinèses somatique. I. Racine de *Trillium grandiflorum* et télophase homotypique dans le *Trillium cernuum*. La Cellule **21**:7–76. 1903.

18. LAWSON, A. A., Studies in spindle formation. BOT. GAZ. **34**:81–100. 1903.

19. ———, The phase of the nucleus known as synapsis. Trans. Roy. Soc. Edinburgh **47**:591–604. 1911.

20. ———, Nuclear osmosis as a factor in mitosis. Trans. Roy. Soc. Edinburgh **48**:137–161. 1911.

21. MOTTIER, D. M., Heterotypic chromosomes. BOT. GAZ. **40**:171–178. 1905.
22. ———, The development of the heterotypic chromosomes in pollen mother cells. Ann. Botany **21**:309–349. 1911.
23. ———, Mitosis in pollen mother cells in *Acer Negundo* L. and *Staphylea trifolia* L. Ann. Botany **28**:115–135. 1914.
24. MOTTIER, D. M., and NOTHNAGEL, MILDRED. The development and behavior of the chromosomes in the first or heterotypic mitosis of pollen mother cells of *Allium cernuum* Roth. Bull. Torr. Bot. Club **40**:555–565. 1913.
25. OVERTON, J. B., Über Reduktionsteilung in den Pollen Mutterzellen einigen Dikotylen. Jahrb. Wiss. Bot. **42**:121–153. 1905.
26. ———, On the organization of the nuclei in the pollen mother cells of certain plants with especial reference to the permanence of the chromosomes. Ann. Botany **23**:19–63. 1909.
27. ROSENBERG, O., Über die Reduktionsteilung im Droserai Neiddel. Stockholms Högs. Bot. Inst. p. 13. 1904.
28. SHARP, L. W., Somatic chromosomes in *Vicia*. La Cellule **29**:297–333. 1913.
29. STOUT, A. B., The individuality of the chromosomes and their arrangement in *Carex aquatilis*. Arch. Zellforschung **9**:114–141. 1912.
30. STRASBURGER, E., Reduktionstheilung. Sitzungsber. Konigl. Preus. Akad. Wiss. **18**:587–614. 1904.
31. ———, Typische und allotypische Kernteilung. Jahrb. Wiss. Bot. **42**:1–70. 1905.
32. YAMANOUCHI, S., Sporogenesis in *Nephrodium*. BOT. GAZ. **45**:7–31. 1908.
33. ———, Chromosomes in *Osmunda*. BOT. GAZ. **49**:1–13. 1910.

## EXPLANATION OF PLATES XXVIII–XXX

All figures were drawn with the aid of a Spencer camera lucida with Bausch and Lomb $\frac{1}{12}$ immersion and ocular 12, except figs. 1–11 inclusive, which were drawn with Bausch and Lomb $\frac{1}{16}$ immersion and ocular 12. Magnification of figs. 1–11 inclusive ×3500; all others ×2650. The plates are reduced to two-thirds the original size.

### *PLATE XXVIII*

FIG. 1.—Late telophase of the last division of the sporogenous tissue, showing the anastomoses and the beginning of vacuolization along the median longitudinal axis.

FIG. 2.—A later stage, most of the chromosomes being vacuolate.

FIGS. 3, 4.—Early stages of the pollen mother cells, which consist of ladder-like structures that arose by vacuolization of the chromosomes; some of the chromosomes still entire, owing to unevenness of vacuolization.

FIG. 5.—Typical resting nucleus of the pollen mother cell; chromatin aggregations comparatively large, and the connecting strands very fine.

FIGS. 6, 7.—Somewhat later stages in which the anastomoses are disappearing, connecting strands between the parallel sides becoming very fine in structure, and the sides of the ladder growing more uniform.

FIG. 8.—Late resting stage; the connecting strands disappearing, leaving two parallel daughter spirems.

FIG. 9.—Early synapsis; the two parallel daughter spirems approaching each other and at places approximating.

FIG. 10.—A later stage; the double nature still plainly discernible in many places.

FIG. 11.—Complete synapsis, showing the coiled spirem in which approximation has been completed.

FIG. 12.—Same as above, but magnification not so great.

FIG. 13.—Coming out of synapsis.

FIG. 14.—Late coming out of synapsis, the double row of granules still visible, these being the remains of the larger chromatin aggregations as seen on the ladder-like structures.

FIG. 15.—Spirem; traces of the granules of early prophase showing.

FIG. 16.—Hollow spirem; granules evident and occasionally a split where approximation was not complete.

*PLATE XXIX*

FIG. 17.—Beginning of second contraction; the spirem very heavy.

FIG. 18.—Second contraction consisting of radiating loops.

FIG. 19.—Segmentation beginning at the outer bend of the loop; *a* and *a'* formerly being continuous, likewise *b* and *b'*; although at this time *a* and *b* are twisting about each other to form the bivalent.

FIG. 20.—Further contraction of the chromatin mass in which the free ends of the bivalents are radiating out from the mass.

FIG. 21.—Loosening up of the bivalents.

FIG. 21*x* and *y*.—Showing the gradual thickening of the bivalents.

FIG. 22.—Eight bivalents evenly scattered within the nuclear cavity in which some are seen to be open at both ends, others closed at one end, while still another, lying under the others, is seen to be stretched out instead of twisted.

FIG. 23.—Beginning of the fiber formation outside the nuclear membrane which accompanies the third contraction; also the disappearance of the nuclear membrane.

FIG. 24.—A slightly later stage; nuclear membrane apparently gone on one side of the nucleus.

FIG. 25.—Later; the fibers in contact with part of the chromosomes; nuclear membrane entirely disappeared; the multipolar complex begun.

FIG. 26.—A later stage.

FIG. 27.—Third contraction complete; fibers have completely filled the nuclear cavity.

FIG. 28.—Multipolar spindle; chromosome aggregation loosening up.

FIG. 29.—Formation of the individual wefts of fibers for each chromosome; the scattering of the bivalents upon the fibers; and a step farther in the transition from multipolar to bipolar spindle.

FIG. 30.—A later stage.

*PLATE XXX*

FIG. 31.—Bipolar spindle; bivalents stretched out upon the fibers.

FIG. 32.—Polar view of early metaphase.

FIG. 33.—Polar view of metaphase with bivalents peripherally arranged.

FIG. 34.—Metaphase in which the individual wefts of fibers are extending from each chromosome to the pole; also the fibers' massive organization at the point of attachment; to the left is a weft that has been broken from its chromosome.

FIG. 35.—Early anaphase; the longitudinal halves of each somatic chromosome that arose by vacuolation in early anaphase are again becoming apparent.

FIG. 36.—Anaphase; halves of the somatic chromosomes entirely separated.

FIG. 37.—Polar view of the same.

FIG. 38.—Late anaphase; 16 half chromosomes approximating end to end to form a spirem $2x$ chromosomes in length.

FIG. 39.—Daughter nucleus after loosening up of chromosomes.

FIG. 40.—Daughter nucleus; irregular net appearance due to the anastomoses.

FIG. 41.—Daughter nucleus; spirem stage in which the fibers of previous mitosis have not disappeared.

FIG. 42.—Daughter nucleus; late spirem in which the outlines of the segments are discernible.

FIG. 43.—A later stage in which the multipolar complex has appeared.

FIG. 44.—Segmentation into 16 segments followed immediately by their pairing.

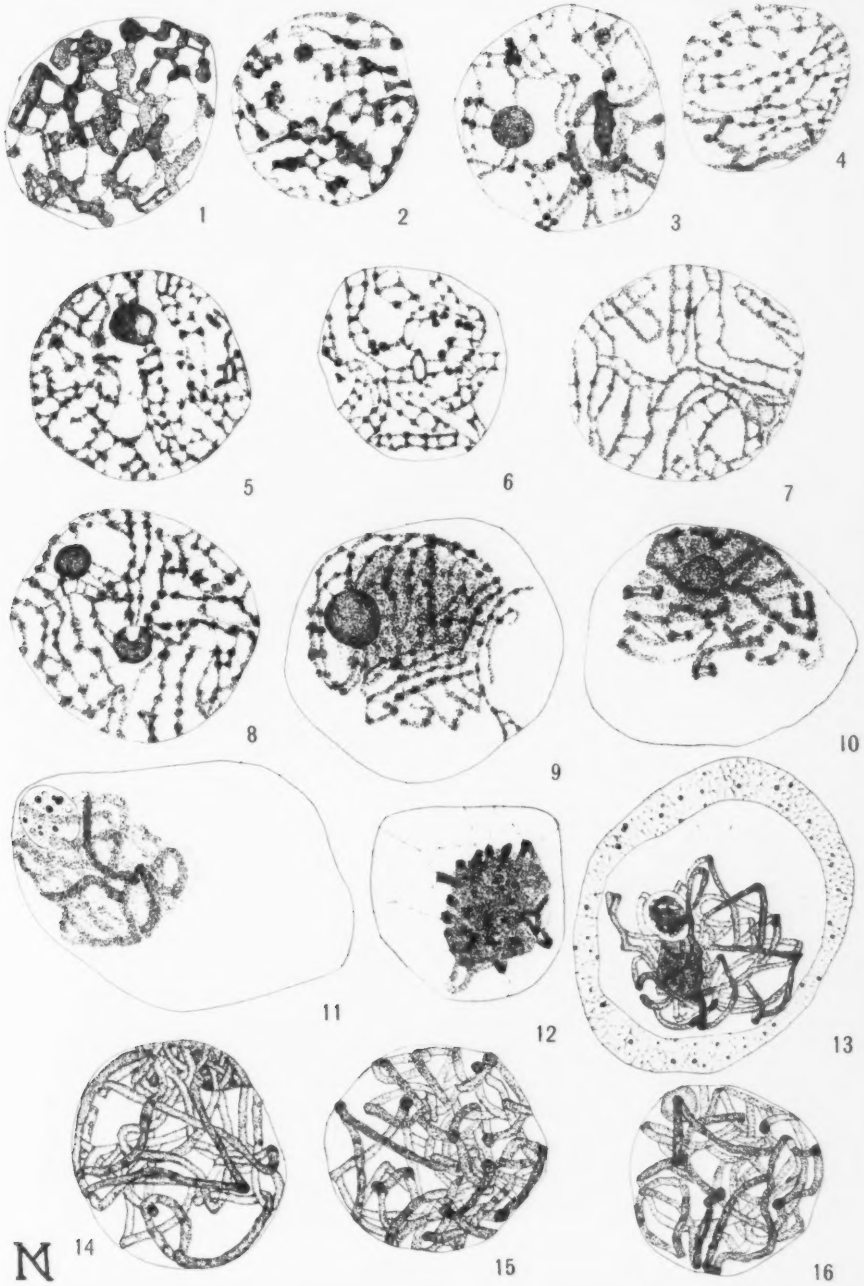
FIG. 45.—Polar view of metaphase of homotypic mitosis.

FIG. 46.—Late metaphase of the two daughter nuclei.

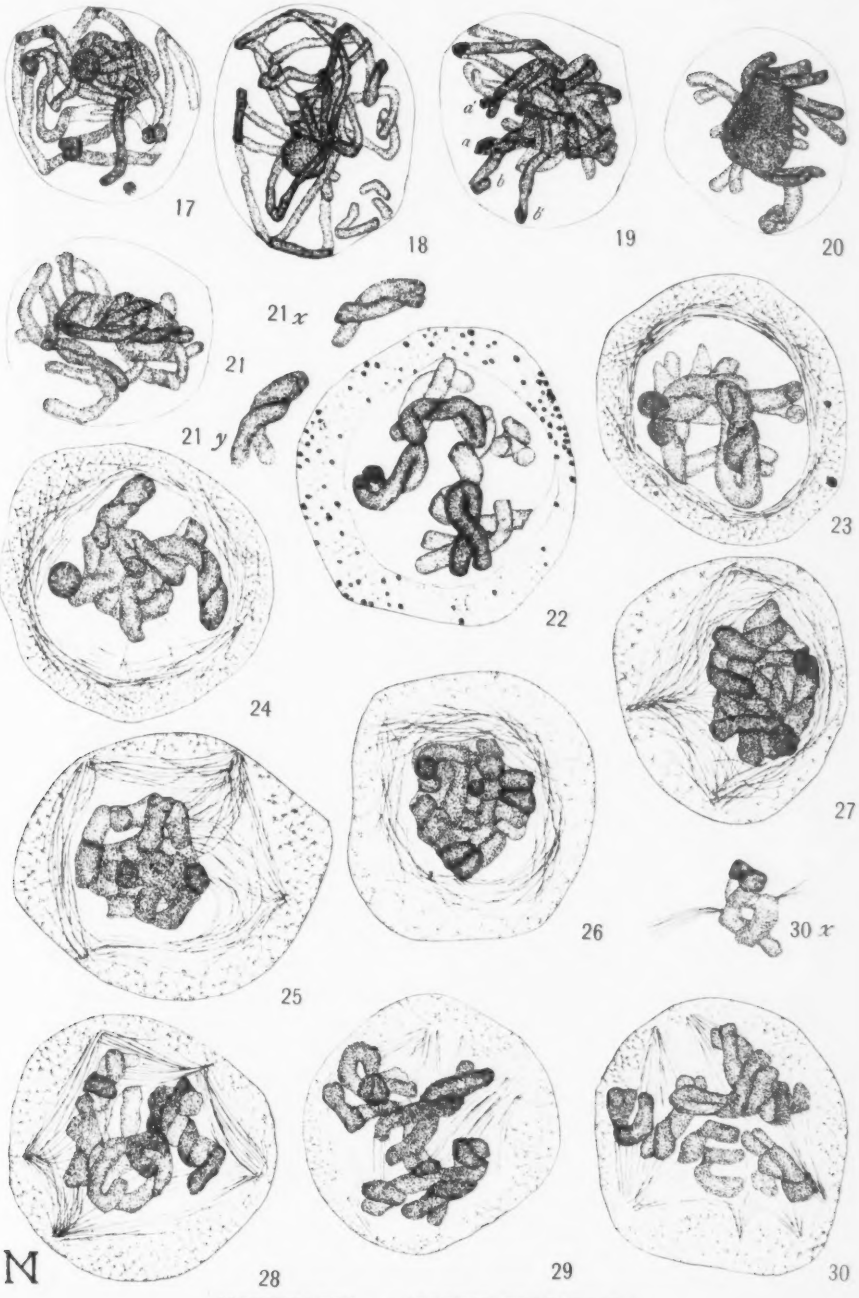
FIG. 47.—Same, but only one daughter nucleus in plane.

FIG. 48.—Anaphase of homotypic mitosis.

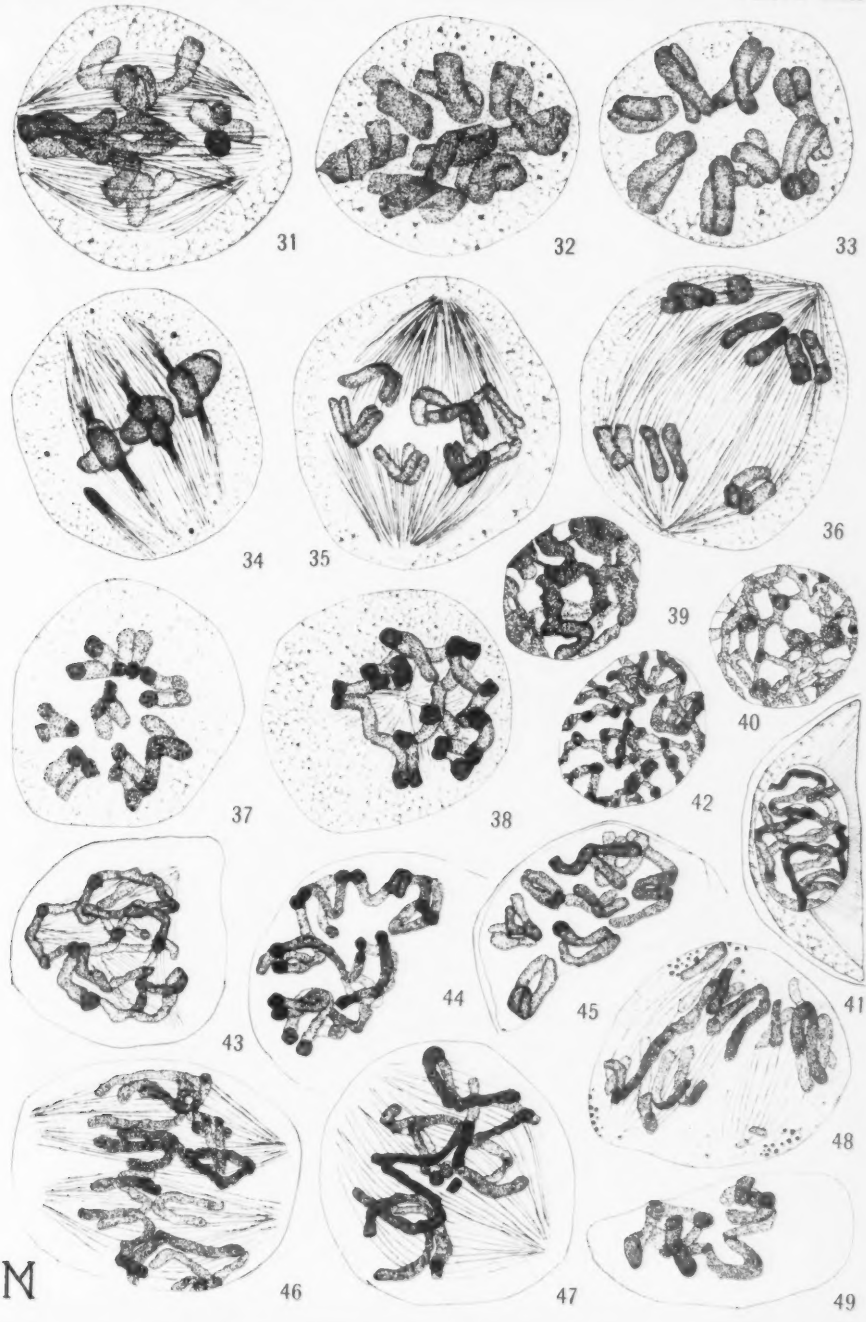
FIG. 49.—Telophase of homotypic mitosis; end to end approximation of 8 chromosomes just previous to organization of granddaughter nucleus.




NOTHNAGEL on ALLIUM TRICOCCUM




NOTHNAGEL on ALLIUM TRICOCCUM




NOTHNAGEL on ALLIUM TRICOCCUM

# THE VEGETATION OF THE SELKIRKS[1]

CHARLES HUGH SHAW

(WITH MAP)

A most attractive region for the study of mountain vegetation is found in the vicinity of the Continental Divide in Western Canada. The mountains, glacier crowned and of the noblest order, are covered in their lower reaches by luxuriant forests. In the higher altitudes are extensive areas where a rich alpine vegetation finds its appropriate home. The region, therefore, is a most attractive field for the botanist, especially since the whole area is as yet practically undisturbed by man. During the last few years the writer has had considerable opportunity for observation there. Base camps have been established at spots thought favorable for the study of the plant life, and quasi-exploring expeditions have been made into districts remote from the railroad. Although only very moderate progress has been made toward a solution of the great questions which present themselves, it was thought that a description of the vegetation as it exists would be of some interest and of value as a record.

[1] This paper has been compiled from Dr. SHAW's notes by one of his students (Miss CAROLINE S. ROMER) who accompanied him on three of his six exploring trips in the Selkirks and who studied the vegetation of the region under his guidance during two of these trips.

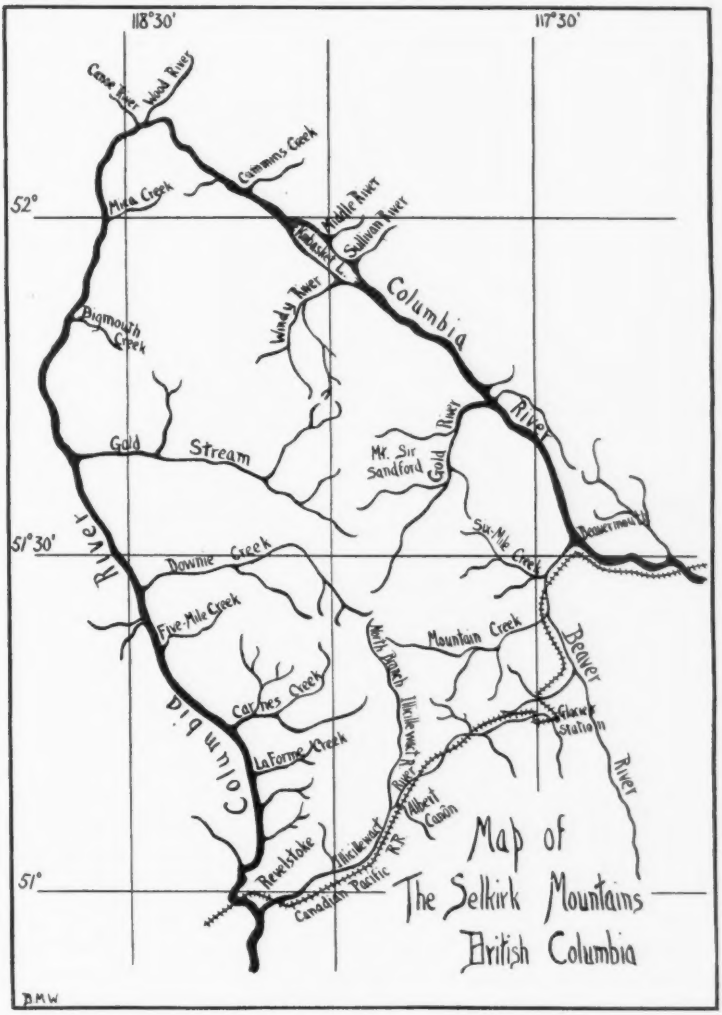
As will be remembered by those botanists who are interested in the development of ecological botany in North America, Dr. SHAW, one of the most earnest and most promising of the younger ecologists, chose as his field of investigation the ecological problems presented by the vegetation of the little known Selkirk Mountains. His work was cut short by his lamentable death by drowning in Kinbasket Lake in July 1910. Extensive notes which he had made during June and July 1910 were unfortunately lost with him. The material that he left comprises, besides many specimens sent to several of the more important herbaria, the introduction to this paper in its present form, and numerous notes concerning the plant life of the Selkirks. To interpret these notes has been no light task. There are doubtless mistakes, errors in interpretation, but, as it seemed to Dr. SHAW's friends and to his fellow-botanists that his work should not be entirely lost, this record of his Selkirk studies has been made as nearly as possible like the record that he expected to make.

## Topography

The general topography of the region will be understood by keeping in mind the course of the Columbia River. The first 500 miles or so of its course are in the form of a huge acute angle whose apex is directed northwest and whose western arm extends southward. The upper or eastern arm flows northwest parallel to the Continental Divide, and the "bend" is just above 52° north latitude. The mountains east of the river and forming the Divide are the Rockies proper; those nearly surrounded by the Columbia, especially those above 51°, are called the Selkirks; while west of the river, and separating its basin from that of Fraser, is the Gold Range. It will thus be seen that the Columbia River rises in the midst of the continental mass of mountains, in the midst also of the cordilleran forest which at this latitude extends from the Great Plains to the dry interior of British Columbia. The area dealt with in the present paper is that of the Selkirks proper, taking 51° north latitude as an arbitrary southern limit; the rest of the boundary being formed, of course, by the river itself. The area thus delimited is practically untouched by human influences. The Canadian Pacific Railway indeed passes through it, and has opened up some wonderful spots to the traveler, but in most places the influence of the railroad has not made itself felt a gunshot from the tracks. North of the railroad there is neither wagon road nor village, store nor post-office, white woman nor child. A scattered line of settlements along the railroad, half a dozen or less inhabited cabins on the river, a mining camp or two, and a few wandering trappers or prospectors constitute the sum of its human influences. From the naturalist's standpoint these have no importance in relation to the broad leagues of wilderness. The phenomena of plant life which may now be seen represent, therefore, the results of conditions operating through a long series of generations, beginning with the last retreat of the ice.

The entire area is extremely mountainous, and in the character of its topography young. The mountains are lofty and precipitous, the streams narrow and swift. Innumerable snowfields and glaciers cover the high summits, tongues of ice not seldom reaching down into the forest. A certain roundness of contour of the lower

mountains contrasts sharply with the more jagged character of the Rockies, but the higher peaks are of the boldest. Although in




absolute altitude the Selkirks are surpassed by many ranges, in elevation of the summits above the valleys they are not easily

equaled. The river and its large tributaries are at altitudes of from 500 m. to nearly 1000 m. The peaks range from 2500 m. to nearly 4000 m. Mountain flanks with a rise of 1000 m. are common, and in certain cases a difference of as much as 2600 m. of altitude occurs within a horizontal distance of two or three miles. Needless to say, such a mountain side presents the most varied forms of vegetation, from tangled forests below to the dwarfed plants of the cold deserts above.

In obtaining an idea of the surface features of the country, it will be helpful to keep in mind again the course of the Columbia. The lakes in which it rises, as well as the first 100 miles of its course, lie in a broad and terraced valley, evidently the site of an ancient lake. Near Donald the river turns abruptly out of this valley into a narrow canyon, and from that point it completes its bend in a series of wild gorges, alternating occasionally with wider and more level valleys. Most interesting problems of captured drainage and reversed flow here await investigation. At one point some 30 miles above the bend, the river expands into Kinbasket Lake. The course of the smaller streams will be apparent from the map. For the most part they descend swiftly as torrents, but in a few places, notably on the Beaver, Downie, and Goldstream, there are portions that have been nearly base-leveled, and in these the activity of the beavers has given rise to extensive swamps.

## Climate

Adequate meteorological records have never been made, but the following may give some idea of climatic conditions.

TEMPERATURE.—This factor varies greatly, of course, in connection with altitude, exposure, etc. At the level of the river, summer temperatures of 33° C. are by no means rare, and once I recorded 38° C. At high altitudes, as is usual, temperatures are always low except at noonday in the direct sunlight.

In the season of 1908 two thermographic records were made on Mount Plainside near Beavermouth on the same hillside and exposure, at altitudes of 800 and 1700 m. respectively. The lower station was about 100 m. above the river level; the upper,

in the midst of the subalpine zone.[2] From these records it is evident that less daily variation occurs at high altitudes. The daily maxima are notably less than those at lower altitudes, the nightly minima only slightly so. This accords well with the general observations of meteorologists.

From records kept at Revelstoke throughout the year, it is possible to gain some idea of the temperature during the winter. The minimum of $-50°$ C., while striking, is probably without significance for vegetation. At higher altitudes, owing to inversion of temperature, the cold is probably much less severe. A registering thermometer was left over the winter of 1908–1909 on the top of Mount Grizzly (3000 m.). When found the following summer, it had every appearance of being in good working order and the recorded minimum was $-1°$ F. Of course, the rocks where the instrument was secured were deeply covered with snow during most of the year.

Occasional frosts occur even at river level in midsummer. Thus, on the night of July 20, 1905, there was a heavy frost in the valley of Goldstream (616 m.). I was unable to learn whether there was frost on the mountain flanks a little higher up or not, but suspect that the low temperature prevailed only in the floor of the valley (a case of temperature inversion).

At and above timber line snow may fall at any season. Each summer there are usually one or two storms in which "new snow" covers the mountains from timber line upward—quite the same phenomenon that is seen in the Alps. Aside from such storms and away from the immediate vicinity of the glaciers, nightly frosts are mostly light and irregular during July and the early part of August (light frost in the alpine meadows is often visible when the thermometer has failed to record freezing). After the middle of August the nights become notably cooler, the nightly frosts become sharper, and by the middle of September they are frequent at all altitudes.

PRECIPITATION.—The volume of precipitation appears to increase from the southeast to the northwest. In the terraced portion of the Columbia Valley, where there are a number of ranches, summer rainfall is so far from that desirable for crops that irrigation

[2] These records are unhappily lost.

will probably be necessary; and although the Selkirks and the Gold Range bear the reputation of being rain-soaked mountains, I suspect that sufficient information would place them in the summer-dry category.

My own data have been obtained in various places, and while on the march. Such items should be numerous and in long series in order to have much value, for showers are often of local occurrence and are more frequent in some localities than in others. A vivid impression of local differences is often conveyed from an outlook point where a wide expanse of peaks is visible. Over most of the landscape there may be sunshine, while Rogers Pass and the great peak in the north, variously called Cloud Summit, Sir Sanford,[3] and the Chieftain, are enveloped in dark rain clouds.

A rough summary of the weather in the growing season for a number of summers is given in table I.

The reputation which the Selkirks bear is probably due partly to the luxuriance of the vegetation, all the more striking to those who come from the thinly forested Rockies, and partly to the fact that very rainy summers have occurred. The accounts of the explorers who found the route for the railroad in the early eighties are tales of great hardship, in which tangled brush and incessant rain are prominent features. Witness also the memorable summer of 1907. So far as data are available, however, it would appear that summer precipitation is scanty, on the whole, and that the climate of the Selkirks resembles that of Puget Sound.

Whatever may be the fact in regard to rainfall, there is another form of precipitation, the regularity and abundance of which is not open to question. Light snows come and go about timber line occasionally during July and August, and more frequently during September and early October, until, by the first of November, the snow mantle is spreading rapidly downward into the forest. From November until the following spring, the whole surface of the earth is deeply covered. At Glacier, altitude 1260 m. as recorded by instrument, 75–150 cm. of snow falls annually. In the subalpine zone the packed snow becomes 2–3 m. deep, not to disappear until June; that at lower altitudes is somewhat less, the

[3] This name has since been adopted.

lightest occurring in the wide valley of the Columbia in the southeast. Such a layer of frozen water, annually renewed, slowly melting, setting free one portion of surface after another, and at the time

TABLE I

| July and August | Number of days on which we met with rain | Comment |
|---|---|---|
| 1904..... | 11 | Rains light, usually for a few hours only; in one case, at Rogers Pass, altitude 1300 m., clouds hung low, with nearly continuous drizzle for 4 days (August 21–26) |
| 1905..... | 9 | Likewise mostly light rains and of short duration; one hail and two thunder storms at 2000 m. and one fall of about 20 cm. of snow August 5 at the same altitude |
| 1906..... | ..... | As stated by my brother, frequent showers but scarcely any heavy enough to cause one to seek shelter; two snows above timber line |
| 1907..... | 35 | From August 3 to September 1 almost incessant rain, much of the time in copious volume; conditions general over the Selkirks, Rockies, and the Gold Range |
| 1908..... | 7 | Only 3 or 4 short showers before August 25; most of the time uniformly fair; conditions general over the Selkirks, Rockies, and Gold Range |
| 1909..... | 13 | Cloudy and rainy during early part of July but no copious precipitation; from July 18 to September 1 and after, prevailingly fair; a snowfall of about 35 cm. at timber line August 4 and 5, a *heavy* shower August 26 |
| 1910..... | 4 | A snowfall at timber line July 15; heavy rains July 21, 22, and 24; no other rains during July and early August |

of its departure leaving the soil laden with all the water it can hold, must be, for vegetation, a most important factor in the physical environment.

## Vegetation

The plant covering of the area exhibits, of course, a wide series of variations growing out of the specific nature of the forms, and out of differences in the surrounding physical factors. How best to study and describe such a vegetation complex is a puzzling matter. Following the broad distinctions of SCHIMPER, we may

designate three formations in the Selkirks: forest, alpine grassland, and alpine desert. The first two interlock, the latter two grade imperceptibly into each other. Within the forest are streams with their distinct plant life, and occasional areas of swamp and bog, as well as cliffs and gravel slides which exhibit desert conditions and to some extent the same species as the alpine deserts. Above the forest there is every gradation, from alpine rivulet to barren cliff. To attempt to reduce all this to a classified and logically complete system of subformations, societies, etc., is a task in which the writer can see neither profit nor hope. The interesting facts and relations which may be observed will be brought out simply as facts.

THE FOREST FORMATION.—The forest covers the entire area up to the timber line at about 1900 m. The most striking feature in its general physiognomy is the increase in luxuriance westward. In the Rockies and southeastern portion of the Selkirks the trees are usually not more than 30–50 cm. in diameter, and 15–25 m. high. In the Columbia Valley from Quartz Creek and the Beaver northward, however, and on all the western slopes of the Selkirks, the forests attain a magnificent development. The trees of various species are commonly 100–150 cm. in diameter and 30–60 m. high, suggesting, though by no means equaling, the marvelous forests of the Puget Sound region. It is scarcely to be doubted that this greater development is bound up with a greater precipitation over the area named. Related facts in regard to the peculiar distribution of certain species will be brought out later.

The forest is further diversified by the effects of fire. Fires have occurred apparently from remote periods, and all phases of succession can be found, culminating in the climax type. The chief cause of the fires seems to be lightning. A tree with a mass of dead resinous branches is a highly inflammable object, and, as a matter of experience, an outlook from a vantage point after a sharp thunderstorm usually reveals one or more slender columns of smoke rising from the forest. Fortunately such fires often die out before much damage is done.

With respect to altitude, the forest is rather plainly composed of two zones, which, in accordance with a usage now happily becoming somewhat uniform, we may designate as the montane

zone and the subalpine zone, the latter beginning at about 1400 m. We shall give attention to the former first.

The montane zone exhibits considerable diversity. The differences between the eastern and the western portions of the area are so strongly marked that the two might easily be treated separately. The hemlock occurs only in the northern and western portions. Quite a series of herbaceous plants (*Lycopodium lucidulum, Chimaphila umbellata, Corallorhiza Mertensiana, Asarum canadense, Circaea alpina*) have been found together only in company with the hemlock, and with it they might be said to constitute a distinct "society" or "formation." But, taking a broader view, we see that, since all these species are found in different combinations in various regions, the fact that they occur together under the hemlocks in the Selkirks indicates no more than that they each respectively sustain a living relation with the physical factors prevailing there. Doubtless the hemlock is very efficient in bringing about the moist and shady conditions in which the others commonly thrive, but further than this it is not apparent how expressions indicating a social interrelationship throw any light on the physiological problems involved. At this point also the interesting fact comes in that almost all the "shade" plants, the ferns excepted, have been found growing in the burns, largely exposed to sunlight.

The following are lists of the more conspicuous or noteworthy species of the montane zone arranged approximately in order of their abundance:

Trees

*Principal species*

Picea Engelmannii
Tsuga heterophylla
Thuja plicata
Pseudotsuga mucronata
Tsuga Mertensiana
Pinus monticola
Populus balsamifera

*Minor species*

Pinus Murrayana
Abies lasiocarpa
Populus tremuloides
Betula papyrifera
Acer glabrum

Shrubs

Alnus tenuifolia
Echinopanax horridum
Salix sp.
Vaccinium membranaceum
Rubus parviflora
Vaccinium ovalifolium
Lepargyrea canadensis
Pachystima Myrsinites
Lonicera ciliosa
Cornus stolonifera
Taxus brevifolia
Ribes echinatum
Ribes lacustre
Rubus strigosus
Spiraea betulaefolia
Corylus rostrata
Crataegus Douglasii (?)

Herbs (including all low forms)

Aspidium spinulosum dilatatum
Cornus canadensis
Kruhsea streptopoides
Vagnera amplexifolius
Rubus pedatus
Linnaea borealis
Tiarella unifoliata
Streptopus amplexifolius
Veratrum viride
Clintonia uniflora
Mitella nuda

Herbs (including all low forms)—*Continued*

Streptopus curvipes
Asplenium Filix-foemina
Phegopteris Dryopteris
Moneses uniflora
Pyrola secunda
Disporum majus
Pteridium aquilinum
Chimaphila umbellata
Fragaria glauca
Equisetum sylvaticum
Lycopodium lucidulum
Circaea alpina
Equisetum arvense
Equisetum pratense
Asarum canadense (acuminatum?)
Habenaria obtusa
Habenaria orbiculata
(Mosses and liverworts in abundance in the deeper forests)

A similar list of species found in an early phase of the reforestation of a burn will show the changes incident to fire:

Trees

*Leading species*

Tsuga heterophylla (2)
Pinus Murrayana (8)
Populus tremuloides (10)

*Less prominent*

Pseudotsuga mucronata
Picea Engelmannii
Pinus monticola
Thuja plicata
Betula papyrifera
Abies lasiocarpa
Populus balsamifera

Shrubs

Salix sp.
Lepargyrea canadensis
Pachystima Myrsinites
Rubus strigosus
Alnus tenuifolia
Vaccinium membranaceum
Rubus parviflora
Cornus stolonifera
Ceanothus ovatus
Amelanchier florida
Lonicera involucrata
Spiraea betulifolia
Ribes echinatum
Juniperus sibirica
Menziesia ferruginea
Viburnum pauciflorum

Herbs

Epilobium angustifolium
Linnaea borealis
Cornus canadensis
Apocynum androsaemifolium
Equisetum pratense
Pyrola secunda
Pteridium aquilinum
Vagnera amplexifolius
Clintonia uniflora
Pedicularis contorta
Pedicularis racemosa
Streptopus amplexifolius
Anaphalis subalpina
Chimaphila umbellata
Galium boreale

Poor specimens of
Phegopteris Dryopteris
Thalictrum occidentalis
Disporum majus

*Picea Engelmannii* is the most generally distributed species of the region. It occurs throughout the area, in the neighboring Rockies, and in the Gold Range, and extends upward into the subalpine. Its relative importance is greater in the southeast and in the Rockies, where it does not come into competition with the hemlock. In the southeast it is usually the most abundant species of the climax forest, although, like other trees in that quarter, mostly of 30–50 cm. diameter and a height of 15–25 m.

*Tsuga heterophylla*, on the other hand, is sharply limited in its distribution. It does not occur at all to my knowledge south or east of the Beaver and Columbia, being therefore quite absent from the Rockies. Within the bend, however, it at once becomes abundant and, growing luxuriantly as it does, may well be said to

dominate the vegetation in considerable areas; but it never entirely excludes the spruce, the mountain pine, and the Douglas fir. Within the area it is one of the most prominent trees of the burns, seeming in this respect like the lodgepole pine.

*Thuja plicata* is, at least in some respects, the monarch of plants in the Selkirks. Occurring sparsely in the Rockies and upper Columbia Valley, it finds its proper home in the deep moist valleys of the western arm of the Columbia. Here it not seldom reaches a diameter of 3 m. The trunk tapers rapidly, however, and is seldom over 50 m. high. Another fact which detracts from its timber value is that the trunks are usually decaye dwithin, a large and sound tree being almost unknown.

*Pseudotsuga mucronata* shows ability to endure and to respond to a wide variety of conditions. As is well known, it reaches a huge development in the Puget Sound country, forming perhaps the most magnificent forests on the globe. Nevertheless, it endures conditions of dryness better than most of the other conifers. It extends south to Colorado and beyond, and in Canada, as one passes from the treeless plain to the foothills, it is one of the first trees to appear. In the region we are studying it is nowhere abundant, yet it occurs throughout. It grows largest on the western slopes of the Selkirks, making there a diameter of 2 m. and a height of 65 m. or more.

*Pinus monticola*, a large white pine, is scattered through the area, nowhere very abundant, but becoming a valuable timber tree in the hemlock district.

*Populus balsamifera* occurs constantly along the river, sometimes forming forests several hundred meters wide. It reaches a diameter of 1–2.5 m. and a height of 30–45 m.

*Pinus Murrayana*, the lodgepole pine, is remarkable both for its limited distribution and for the part it plays in reforestation. In all the region where it occurs it is the first tree to spring up after a fire. In the Rockies particularly, the burn forest is often almost purely lodgepole pine. Its range is sharply confined to the Rockies and the drier portion of the Selkirks, ceasing rather abruptly where the hemlock begins. The cause of the peculiar distribution is not wholly clear. Possibly it cannot survive in

competition with the hemlock, and is confined therefore to areas where the latter cannot flourish on account of dryness. Possibly, also, the lodgepole pine has not been able as yet to cross the central mass of the Selkirks, nor to make its way from burn to burn around the bend. It certainly would have little chance to invade the climax forest.

*Populus tremuloides* is another prominent member of the burn vegetation, universally distributed, growing in company either with the lodgepole or the hemlock, as the case may be.

*Abies lasiocarpa* occurs sparingly in the montane forest. It is rarely to be seen near the river, but is one of the 3 or 4 species forming the tree clusters on exposed ridges.

The birches, maples, buckthorns, and hazels are found only along the river and the lower waters of its tributaries, and are usually not abundant.

In the moist river-level forests, especially along the western arm of the river, and in such moist pockets as that found at the foot of Mount Cheops at Rogers Pass, certain shrubs grow in remarkable luxuriance. Among these the most conspicuous are: in the river-level forests, *Echinopanax horridum*, *Taxus brevifolia*, *Corylus rostrata;* in the moist pockets, *Vaccinium ovalifolium*, *Rhododendron albiflorum*, alders, and willows. In the moist, well shaded river-level forests, especially along the Columbia between Bigmouth and the great angle made by the Columbia, vegetation reaches a marvelous degree of luxuriance. Here careful measurement indicated that the following spermatophytes and pteridophytes reached a height of 2.50–3 m.: *Veratrum viride*, *Echinopanax horridum*, *Vagnera amplexifolia*, *Pteridium aquilinum*, *Aspidium spinulosum dilatatum*. Here also the mosses *Hylocomium proliferum* and species of *Thuidium* covered the rocks and fallen tree trunks with thick cushions of exquisite foliage.

THE ALPINE MEADOW FORMATION.—As previously stated, the alpine meadow and the forest formations interlock, the former frequently extending far down below the timber belt in the depressions, while the latter reaches upward on the exposed mountain flanks and ridges. The bulk of the alpine meadow vegetation lies between 1800 and 2500 m. The plant associations vary greatly,

of course, according to altitude, topography, exposure, and moisture content of the soil.

Almost as important as altitude in determining the character of the vegetation of a given area are topography and exposure to light. While crags and ridges may be free from snow in May or early June, the depressions between them frequently lie buried under snow until the middle or latter part of July. These masses of wet snow are apparently responsible for the drowning and suffocation of the trees and larger shrubs in these depressions, as I suggested in an earlier paper.[4] Other things being equal, the snow disappears first from the east-facing and south-facing slopes; these slopes therefore usually bear a more luxuriant and more varied vegetation than those facing the west and north. It would seem that, in the Selkirks, long-enduring snow masses, caused by heavy winter precipitations, topography, and exposure of the mountain slopes, are the most important single factor in determining the distribution of the alpine meadow and alpine desert vegetation.

Among the trees which reach in scattered groups into the alpine meadows, thus forming true "parklands," firs and spruces predominate. At 1800 m., in the lower portions of the belt, these retain their characteristic conical form and frequently reach a height of 7 m. They are found most abundantly and are grouped most effectively on slight elevations surrounding the numerous alpine tarns of this newly glaciated country. At higher elevations, reaching even to 2500 m., the firs and spruces exhibit the forms of wind and snow cripples. Here they are associated with dense thickets of juniper, and with occasional groups of the white-stemmed pine (*Pinus albicaulis*). The thickets often cover the broader mountain flanks, the gnarled cripples appearing in smaller groups or singly on crags and narrow "sawbacks." An examination of the rings of wood in the trunks of some of these cripples gave evidence, as was to be expected, of extremely slow growth. Thus a fir, 40 cm. in height and 2.5 cm. in diameter of trunk, cut near the summit of Glacier Crest, between the Illicillewaet and Asulkan glaciers, showed 62 wood rings.

[4] SHAW, C. H., The causes of timber line on mountains. Plant World 12: *figs. 4.* 1909.

Such shrubs as show any considerable length of stem commonly lie prostrate, thus giving evidence of the crushing effect of the masses of snow that cover the lower meadows during 9 or 10 months of each year. Of these *Rhododendron albiflorum* and *Vaccinium membranaceum* are most frequently met with on the lower slopes, especially on those threaded by rivulets originating in snow banks higher up. Farther up the slopes, and reaching quite to the alpine deserts, dwarf willows, *Arctostaphylos Uva-ursi*, *Cassiope Mertensiana*, *Empetrum nigrum*, *Bryanthus glanduliflorus*, *B. empetriformis*, *Gaultheria myrsinites*, *Kalmia glauca*, *Dryas octopetala*, and occasionally *D. Drummondii* are the dwarfed shrubs. These sometimes form small patches in the grassland; sometimes they form extensive carpets covering many square meters. Mats of *Cassiope* or of *Bryanthus* or *Dryas* form dry hummocks in comparatively wet meadows. As these mats enlarge year by year, the plants at the center die, thus bringing about the formation of rings of shrubby growth surrounding dead and blackened centers. This seems to bear out SCHROETER'S statement:[5] "Das dichte Heidekrautgestrüpp erzeugt einen ganz eigenartigen, schwarzen, nährstoffsarmen Humus, der eine Menge von Arten ausschliesst."

Moisture and the presence or absence of snow covering during the short growing season seem to be the principal factors determining the nature of the herbaceous vegetation of the alpine meadows. On very wet slopes and depressions, where the ground is continually soaked by water from the melting of the snow fields higher up, there are commonly either nearly pure stands or mixed associations of the following: *Ranunculus alpinus*, *Trollius albiflorus*, *Caltha Macounii*, *Lutkea pectinata*, *Valeriana Scouleri*, and *Erythronium grandiflorum*. With these are associated, in lesser quantities, *Mitella nuda*, *Petasites frigida*, *Oxyria digyna*, *Rumex crispus*, *R. acetosella*, *Parnassia parviflora*, *P. fimbriata*, *Saxifraga rivularis*, *S. Lyallii*, *S. nivalis*, *Thalictrum occidentale*, *Epilobium angustifolium;* numerous sedges and grasses, among them *Carex invisa*, *C. nigricans*, *C. livida*, *Poa arctica*, and *P. alpina*. The stretches of *Erythronium* and of *Trollius*, varied by very intruding plants of

[5] SCHROETER, C., Das Pflanzenleben der Alpen.

other species, are especially beautiful and interesting. Occasionally one comes upon fields, several acres in extent, consisting apparently of nothing but the swaying yellow bells of *Erythronium*. Some of the smaller basins, where the snows have but recently melted, are entirely filled with *Ranunculus alpinus*, which often blooms under the shallow snow water. Of the principal species, *Trollius*, *Valeriana*, and *Erythronium* are commonly found together; while *Lutkea*, *Ranunculus*, and *Caltha* form another and quite distinct association. As the slopes become drier, cushion plants of various species may be associated with these plants. Of these the most abundant are *Silene acaulis*, the two species of *Dryas*, the saxifrages, the heathers, sedges, and grasses.

On the mesophytic grasslands, *Pulsatilla occidentalis* is the dominant plant. Large fields and gentle slopes covering hundreds of square meters often bear *Pulsatilla* to the exclusion of all other vegetation. Where this condition obtains, its chief cause is always in evidence, namely, scores of burrows of the ground squirrels that delight to line their homes with the plumed fruits of the *Pulsatilla*, thus assuring the reproduction of the plant. When *Pulsatilla* does not form a pure stand, it is most frequently associated with several alpine grasses, *Poa alpina*, *P. arctica*, *P. Cusickii*, *Phleum alpinum*, with *Juncoides parviflora*, *Carex festiva*, and *C. marcida;* and with *Castilleia miniata* and *C. pallida* (running into numerous variations in color and form), *Lupinus perennis*, *Valeriana sitchensis*, *Erigeron jucundus*, *E. salsuginosus*, *Epilobium Hornemanni*, *E. anagallidifolium;* as well as with occasional clumps of heather (*Bryanthus* and *Cassiope*) and of dwarf willows. These plants commonly grow in remarkable luxuriance, and in August, when most of them are in bloom, the brilliant colors of species of *Castilleia*, *Erigeron*, *Epilobium*, and *Lupinus* give to the alpine fields a beauty not readily forgotten by anyone who has had the good fortune to see it.

On the gravel slopes and flats of the youngest terminal moraines a great variety of physical conditions obtains. As to moisture, the range is from wet areas where the glacial streams form pools or bogs, to the sun-baked flats no longer reached by these streams. Here the soil appears at the surface, there it is covered by gravel

and boulders to a depth of a meter or more. Exposure to light is almost invariably extreme. Many of the gravel slopes and flats come properly within the alpine meadow zone. Their vegetation varies, of course, with the physical conditions under which it must exist. The xerophytes grow always in isolated clumps or cushions; the hydrophytes and mesophytes either in clumps or in fairly extensive beds. The xerophytes most in evidence are: *Erigeron aureus*, *Antennaria lanata*, *Kalmia glauca*, *Arnica latifolia*, *Epilobium angustifolium*, *Potentilla emarginata*, *Gentiana prostrata*, *Dryas octopetala*, *D. Drummondii*, *Eriophorum polystichium*, *Calamagrostis purpurascens*, and *Cryptogramma acrostichoides*. A number of these species are found also on the alpine desert. This does not seem remarkable if one considers that, except for increased cold and snow, the conditions under which the desert plants exist are similar to those endured by the morainal xerophytes.

The hydrophytes and hydromesophytes of the moraines are numerous. They often form dense masses of vegetation along the streams, especially on the more level flats. The species found, named approximately in order of abundance, are as follows: *Trollius albiflorus*, *Claytonia lanceolata*, *C. parviflora*, *Rumex crispus*, *Oxyria digyna*, *Caltha Macounii*, *Ranunculus Eschscholtzii*, *Petasites frigida*, *Thalictrum occidentale*, *Parnassia fimbriata*, *Carex nigricans*, *Veronica Wormskjoldii*, *Castilleia miniata*, *Mimulus Lewisii*, *M. caespitosus*, *Epilobium latifolium*, *Eriogynia pectinata*, *Leptarrhena amplexifolia*, *Saxifraga Lyallii*, *S. rivularis*, *S. Nutkana*, *Tiarella unifoliata*, *Aquilegia columbiana*, *A. flavescens*, *Silene acaulis*, *Delphinium Menziesii*, *Anemone Drummondii*, *Parnassia parviflora*, *Erythronium grandiflorum*, *Veronica americana*, *Pedicularis bracteosa*, *P. racemosa*, *Pinguicula vulgaris*, *Epilobium Hornemanni*, *Erigeron jucundus*, *E. multiradiatus*, *E. salsuginosus*, *Comarum palustre*, *Myosotis alpestris*, *Cynoglossum boreale*, *Apocynum androsaemifolium*, *Gentiana glauca*, *Gaultheria humifusa*, *Ligusticum apiifolium*, *Valeriana sitchensis*, *Aster conspicuus*, *Habenaria hyperborea*, *Senecio triangularis*, *Veratrum pedicularis*, *Rhododendron albiflorus*, *Kalmia glauca*, *Elephantella groenlandica*, *Potentilla emarginata*, *Prunella vulgaris*, and *Sibbaldia procumbens*.

THE ALPINE DESERT.—Here low temperatures, snow, and the avalanches due to these are evidently the controlling ecological factors. It is necessary to distinguish between the deserts due to cold and snow, and those due to rock avalanches. The latter are either absolute deserts because recurring avalanches have covered the soil of the slopes with rock to such a depth that vegetation is impossible, or they show isolated plants or cushions of plants where rock covering chances to be shallow. These comprise very few species, *Gentiana prostrata*, *Erigeron aureus*, *Silene acaulis*, *Potentilla* (*emarginata?*), *Epilobium latifolium*, and *Cryptogramma acrostichoides* being the only species found very commonly in these locations. All of these rock desert plants are, of course, extremely small, tough, and dry; their blossoms often impress one as being of unusual size and brilliancy in contrast with the dwarfed and dull green foliage and stems. Since these plants secure moisture only with difficulty, and endure the strong insolation and the desiccating winds of the exposed rock slides, they are to be designated without question as xerophytes, a designation usually supported by such structural characteristics as have just been suggested.

The snow and cold deserts of the high altitudes are peculiarly interesting. At the surface and immediately beneath the surface of the snow, especially on the more extensive snow fields, many thousands of plants of *Sphaerella nivalis* give to the snow exquisite rose and lavender tints. In the Selkirks the alga never has the green color which SCHROETER reports that it shows on the alpine snows. With *Sphaerella* there is frequently associated a fungus which spreads its dark brown, branched mycelium over the surface of the snow. Except for these two plants, the Selkirk snows seem to be truly bare of plant life.

On those high slopes where snow patches remain practically throughout the summer, and where the ground between the patches is free of snow during a few weeks only, a very definite succession is always to be discerned. Very near the snow, surrounding the melting snow patches, there is a black mud with knobby surface evidently covered with fungus mycelia; farther back from the edge of the snow, tiny patches of *Polytrichum* appear. As the clumps of moss increase in size, we find it associated with small bunches

of *Carex nigricans*, which increase in size as we recede from the snow until they form a continuous ground covering. Thus far the succession is invariable; but the plants that grow in scattered groups in the stretches of *Carex nigricans* at some distance from the snow patches may be *Carex invisa*, *Epilobium latifolium*, *Petasites frigida*, *Caltha Macounii*, *Oxyria digyna*, *Parnassia parviflora*, or a *Ranunculus*. When one or more of these plants have joined *Carex nigricans*, conditions no longer warrant the designation of "desert" to this association, but it merges into the hydrophytic or hydromesophytic group, for moisture from the melting snow patches is, of course, abundant in these situations. The term "desert" as applied to the fungus-moss-sedge association bears with it none of the usual suggestions of dryness and heat, but, on the contrary, connotes abundant moisture but physiological dryness due to extreme cold. It is to be remembered in this connection that the suffocating action of the snow, previously mentioned, is here a potent cause of the poverty of plant life.

# STUDIES IN THE GENUS BIDENS. III

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 216

EARL E. SHERFF

(WITH PLATE XXXI)

**Bidens attenuata,** sp. nov.—Herba (annua?), +4 dm. alta; caule et ramis hispido-tomentosis, subtenuibus, subperspicue striatis, teretis (nisi caule infra angulato). Folia opposita (aut superiora alternata), petiolata, petiolo adjecto 1.5–6 cm. longa, bi- aut tri- (aut etiam quadri-) pinnata, subsparsim adpresso-hispida, hispido-ciliata; ultimis lobulis integris, linearibus, indurato-apiculatis, saepe convolutis, 0.3–0.7 mm. latis. Petioli 3–11 mm. longi, hispidi, ad basim connati. Capitula terminalia, ligulata, longe et tenuiter pedunculata, pedunculis 5–15 cm. longis. Involucrum basi hispidum; squamis duplici serie dispositis; exterioribus (circ. 6) linearibus, glabratis aut sparsim hispidis, 3–4 mm. longis; interioribus dimidio longioribus, dense hispidis, margine diaphanis. Ligulae flavae, striatae, elliptico-ovatae, ad apicem subdentatae aut integrae, 1.8–2 cm. longa. Paleae lineares, margine diaphanis. Achaenia (submatura) linearia, glabra, costata, biaristata aristis retrorsum hamosis (3–6 glochidiis), 5 mm. longa.

*Ghiesbrecht*, Chiapas, Mexico (type in Herb. Gray).

ASA GRAY had labeled this plant in the herbarium "*B. ferulaefolia* var.," but the true *Bidens ferulaefolia* DC. (*Coreopsis ferulaefolia* Jacq., Hort. Schoenb. 3:65. *pl. 375.* 1798) is a very different plant.

**Bidens Andrei,** sp. nov.—Herba (ad basim suffrutescens?), 1–2 m. alta, glabrata, caule tetragono et striato; ramis tetragonis, striatis, (superioribus) irregulariter arcuatis et in nonnullos ramulos (aut pedunculos) divisis. Folia opposita, petiolata, petiolo adjecto 2.5–7 cm. longa, bi- aut tri- (aut quadri-) pinnata, supra minute et non dense adpresso-hispida; ultimis segmentis linearibus, integris aut lobulatis, indurato-apiculatis. Petioli 0.3–2 cm. longi, basi connati. Capitula multa, tenuiter pedunculata, pedunculis 4–12 cm. longis, 0.4 cm. (ad anthesin) –1 cm. (in fructu)

alta, ligulata. Involucrum basi plus minusve hispidum; squamis duplici serie dispositis et demum reflexis; exterioribus (circ. 6) linearibus, apiculatis, subsparsim pubescentibus, 1–2 mm. longis; interioribus lanceolatis, membranaceis, 2–3 mm. longis, margine diaphanis. Ligulae (6 aut pauciores) lanceolatae, 4–5 striatae, apice integrae, 3–4 mm. longae, in sicco specimine subalbae. Paleae lineares, margine diaphanae. Achaenia attenuato-linearia, supra sparsim hispida, biaristata aristis glabris aut retrorsum 1–3-hamosis, (interiora) demum 0.8–1 cm. longa.

*Ed. Andre* 2878, at altitude of 1250 m., Rio Juanambu, United States of Colombia, April 28, 1876 (type in Herb. Gray).

The 20–30 areolae on the old disks become prominent as the involucres reflex. There are 37 heads on the type specimen. The plant appears to be entirely herbaceous, but the label says "suffrutesc.," hence the lower part of the plant (not present on the sheet) may have been woody and perennial.

**Bidens mirabilis,** sp. nov.[1]—Herba volubilis glabra, caule subtereto, striato. Folia caulis petiolo adjecto 8–10 cm. longa, pinnata, foliolis irregulariter 3- vel 5-partitis, segmentis (ad marginem sparsim hispidis) ovatis et integris aut ad apicem 1–5 dentatis, petiolis 3–3.5 cm. longis; folia ramulorum parva, integra aut ternata. Capitula (floribus flavescentibus e Sprucei inscriptione) multa, parva, dense paniculata, discoidea, 3–5 mm. lata, 4–5 mm. alta. Involucrum glabratum, squamis duplici serie dispositis; exterioribus lineare-lanceolatis, laciniato-ciliatis, 1.5–2.5 mm. longis. Paleae lineares, 4–5 mm. longae, marginibus diaphanis. Stilorum rami breves, crassi, plus minusve obtusi. Achaenia late cuneato-lanceolata, plana, margine lobulata, lobulis coronatis 1–4 longis pilis; constricta ad apicem cervice crassa, 8–10-aristata aristis inaequalibus et retrorsum hamosis.

*Spruce* 6273, Huambalpa, Andes Mountains, Peru ("Andes Quitenses, loco Huambalo"), November 1857 (type in Herb. Kew). Plate XXXI.

This is a very strange species and one that might be taken by some to represent a new genus; indeed, I know of no other species of *Bidens* combining

[1] Dr. J. M. GREENMAN (now of the Missouri Botanical Garden), to whom I shall express more extended thanks later for having inspired my research upon the genus *Bidens* and directed it during its early stages, and Dr. B. L. ROBINSON (of Gray Herbarium) have very kindly assisted me with certain library and herbarium data for this species.

more diverse characters. The twining habit is to be met with in *B. rubifolia* and its allies; the large number of achene awns (very rarely so numerous in *Bidens*) suggests a certain African species of *Bidens*, to be treated later; the shape of the achenes is rather that of *B. tripartita* and its allies; but the thick, necklike constriction at the apex of the achenes and below the awns is so pronounced as to suggest a slight affiliation with *Heterospermum*,[2] in which genus the outer, *winged* achenes are frequently so constricted.

BIDENS PILOSA L. Sp. Plant. 832. 1753.—*Bidens hispida* H.B.K. Nov. Gen. **4**: 237. 1820; *Bidens andicola* H.B.K. var. *B*, Wedd. Chlor. And. **1**:70. 1855.

For many years, *Bidens hispida* H.B.K. appears to have remained a comparatively unknown form to botanists dealing with South American plants. WEDDELL'S treatment of it is short and arbitrary. No reasons are given by him for its reduction to *Bidens andicola* H.B.K.

The original type plant of *Bidens hispida*, as also that of *Bidens andicola*, remains in good preservation today (in Mus. Hist. Nat. Paris). In a very general way the two plants, both of them hispid, show a resemblance; but *Bidens hispida* is seen, on closer inspection, to have small heads and these, moreover, are discoid. Also, the lower part of the plant displays a wholly different foliage aspect from that found in more recent specimens of the yellow-rayed *B. andicola* (the lower part of the type for the latter species is lacking). The plant is seen to be merely a very hispid form of *B. pilosa* L. It is matched more or less exactly by many specimens in herbaria, particularly by some from Venezuela, Colombia, and Peru (for example, *Mr.* and *Mrs. J. N. Rose* 18740, Santa Clara, Peru, July 18, 1914, in U.S. Nat. Herb.).

BIDENS ANTHRISCOIDES DC. Prodr. **5**:600. 1836.

DECANDOLLE'S description of this species, based upon *Berlandier* 1010 and 1152, is much too narrow not to mislead. Excellent specimens of *Berlandier* 1010 are in London (in Herb. Brit. Mus.),

[2] A genus very closely connected with *Bidens* through *Heterospermum Xanti* Gray, the type of which (in Herb. Gray) is matched by that of *Bidens Xantiana* Rose (in U.S. Nat. Herb.); a species best retained in *Heterospermum*, a view in accord with the treatment by BRANDEGEE (Zoe **1**:309. 1890), who, moreover, has since *positively* corroborated (in litt. 1913) my equation of *Bidens Xantiana* Rose with *Heterospermum Xanti* Gray.

and these have some achenes 21 mm. long. *Berlandier* 1010 and 1152 both occur in Paris (in Herb. Mus. Hist. Nat. Paris and in Herb. E. Drake). These surpass the London specimens in that they show some of the heads to be radiate in anthesis (cf. DC. *l.c.*, "cephalis discoideis"). The flowering heads are small, about 9 mm. high and 4–5 mm. wide, or, including the rays, 1 cm. wide. The rays are small, strongly and definitely dark-roseate, about 5 mm. long (including the tube at base), broadly ovate-elliptic, somewhat 3-toothed at apex. The 8 outer bracts average about three-fifths of the length of the inner ones and tend to be indurate-tipped.

BIDENS NODIFLORA L. Sp. Plant. 832. 1753.—*Bidens nodiflora, brunellae folio* Dillen. Elth. 52. *pl. 44. fig. 52.* 1732: non *Bidens nodiflora, folio tetrahit, ibid.* 53. *pl. 45. fig. 53.*

A good specimen preserved in the Linnaean Herbarium matches the first figure of DILLENIUS very closely and is a true *Bidens*. Recently, DRUCE (The Dillen. Herb. 161. 1907) has cited this figure erroneously, as representing, along with *pl. 45. fig. 53* (Dillen. *l.c.*), *Synedrella nodiflora* (L.) Gaertn., a species treated by LINNAEUS (Amoen. Acad. **4**:290. 1759) as *Verbesina nodiflora*, and which is not at all a *Bidens*. DRUCE, as is indicated by his use of an asterisk, had not seen a Dillenian specimen matching *pl. 44. fig. 52*, but he referred to the *Index Kewensis* as his authority. However, an examination of that work (Ind. Kew. **1**:301 and **2**:1025. 1895), with proper regard for the kinds of type there employed, shows that *Bidens nodiflora* and *Synedrella nodiflora* are retained as distinct species and are not equated.

BIDENS FRONDOSA L. Sp. Plant. 832. 1753.—*Bidens melanocarpa* Wieg. Bull. Torr. Bot. Club **26**:405. 1899.

GREENE (Pittonia **4**:246. 1901) has given a good survey of pre-Linnaean authors and their treatment of the plant finally named *Bidens frondosa* by LINNAEUS. As additional evidence of the accuracy of GREENE'S conclusions regarding the characters of true *B. frondosa* L., there are the three specimens of LINNAEUS (two in Herb. Linn. and one in Herb. Hort. Cliff. at Herb. Brit. Mus.) and one of VAILLANT (in Herb. Mus. Hist. Nat. Paris). The first one of these has a flowering head with 9 or 10 elongate, foliose, exterior

involucral bracts (cf. Linn. *l.c.*, "calycibus frondosis") and "*HU* 4, *frondosa*" is written on the sheet.[3] Pinned with this sheet is a second sheet having a plant without label, but which is coarser and has about 14 exterior involucral bracts on the largest head. The third specimen is among the *Hortus Cliffortianus* specimens and matches the first specimen, even to having the same elongate foliose type of exterior bracts. LINNAEUS clearly had the first or the third specimen, and probably both, in mind when he drew up his description of *B. frondosa* for the *Species Plantarum*. The second specimen is probably *B. vulgata* Greene, but it is not labeled, and has no historical significance. The fourth specimen is the one formerly in VAILLANT'S private herbarium. This last matches the two labeled Linnaean specimens perfectly. Bearing, as it does, in VAILLANT'S own handwriting, the early names[4] afterward cited by LINNAEUS as synonyms for *B. frondosa*, it shows that VAILLANT, himself a student of the genus *Bidens*, likewise understood this species to be the smaller headed, fewer bracted, less robust form (and not the *B. vulgata* of GREENE).

BIDENS CHINENSIS Willd. Sp. Plant. **3**:1719. 1800.—*Bidens pilosa* L. var. *B* Murray, Syst. Veg. ed. 13. 610. 1774; *Agrimonia molucca*, Rumph. amb. **6**:38. *pl. 15. fig. 2.* 1750; *Chrysanthemum chinense*, etc., Plukenet, Phytograph. *pl. 22. fig. 4.* 1691; *idem* Almag. Bot. 100 (excl. syn.). 1696; *Bidens cicutaefolia* Tausch, Flora **19**:395. 1836.

Recently, O. E. SCHULZ (Engl. Bot. Jahrb. **50**: Suppl. 176. 1914) has presented a good historical summary of this species with a comprehensive mass of synonomy. He shows clearly that the name *chinensis* harmonizes in its application with the *chinense* of PLUKENET given over a century before. Evidently, however, he was unaware that the plate of PLUKENET'S *Phytographia* (*loc. cit.*) was the identical plate cited in 1836 by TAUSCH (*Flora*, *loc. cit.*) as the basis for *Bidens cicutaefolia;* and that thus one of TAUSCH'S

[3] Dr. B. DAYDON JACKSON, of the Linnaean Herbarium, assures me that "HU" was used by LINNAEUS to indicate that the plant was raised "*in Horto Upsalensi.*"

[4] I am indebted to Professor P. DANGUY (of the Herb. Mus. Hist. Nat. Paris) for comparisons made with VAILLANT'S known writing to verify the authenticity of these names. An extra label on the sheet "*Bidens frondosa* L." was written, according to Professor DANGUY, by LAMARCK.

ill-advised names, so long apparently enigmatic to botanists, is clearly reducible to synonomy.

BIDENS HUMILIS H.B.K. Nov. Gen. 4:234. 1820.—*Bidens decomposita hirsutior* C. B. Clarke, Compos. Ind. 141. 1876.

Clarke described his variety *hirsutior* from a single specimen collected by himself at an altitude of over 2200 m. in the Nilgiri Mountains of India. Later, he informed J. D. HOOKER (cf. Fl. Brit. Ind. 3:310. 1881) that he supposed it to be some cultivated plant. HOOKER admits having seen no specimen of it, but it happens that CLARKE'S own original specimen ("11207 . . . . 23 March 1870 . . . . coll. *C. B. Clarke* . . . .") was sent to Kew Herbarium in 1877 and is still there in good condition. The plant is very different from *Bidens decomposita* Wall., but differs from certain South American specimens of the highly variable *B. humilis* H.B.K. only in being rather villous. Yet in the same region Dr. WATT collected material (*Watt* 2160, Metapollium, Nilgiri Hills, Southern India, up to nearly 1000 m., June 1876, in Herb. Kew) that agrees with CLARKE'S specimen except that it is minutely pubescent as to leaves and glabrous as to stems. And, most fortunately, still two more specimens from this region occur (*Dr. Thomson*, Eclipse Exped., Nilgiris, December 1871, determined on sheet as "*Bidens humilis* H.B.K.," in Herb. Kew; and *R. H. Beddome* 4511, "introd.? a common weed," Nilgiris, in Herb. Brit. Mus.), both glabrous and indistinguishable from *B. humilis*. A study of these several specimens, all collected in the same region at about the same time, and by two of the collectors suspected of being introduced, shows beyond doubt that they were merely forms of *B. humilis* H.B.K. brought, perhaps in ballast, from South America to the southwest shores of British India.[5]

BIDENS CRITHMIFOLIA H.B.K. Nov. Gen. 4:234. 1820.—*Bidens delphinifolia* H.B.K. *loc. cit.*

The two type specimens from which KUNTH described *B. crithmifolia* and *B. delphinifolia* are still extant in good condition (in Herb. Mus. Hist. Nat. Paris). They differ only in the slightly diverse

[5] Since the above was written, I have had access to the very recent work of FYSON (Fl. Nilgiri and Pulney Hill-tops above 6500 feet 1:237. 1915). It is most interesting to find that FYSON, though omitting historical details, lists *B. humilis* from South America as an introduction into the Nilgiri Hill region, thus adding unique corroboration to my own conclusions presented above.

foliage. The immature type of *B. crithmifolia* is matched exactly by *J. Triana* 1374 (*ibid.*), a specimen from Bogota, Colombia, which is superior in showing not only flowering heads but also numerous achenes. These achenes are mainly 2-aristate, but some are 3-aristate and so agree perfectly with achenes of *B. delphinifolia*.[6] Fortunately, I have found another specimen by *Triana* of the same number in the British Museum, and this shows the slightly different foliage of *B. delphinifolia*, thus removing all doubt as to the identity of *B. delphinifolia* with *B. crithmifolia*.

This species is exceedingly variable in foliage. *Triana* 1375 (in Herb. Brit. Mus.) shows one plant with leaves tripartite, the leaflets being incisely dentate, and another plant with simple, ovate-lanceolate leaves. In fact, the sheet of *Triana* 1374 in Paris bears another specimen (beside that cited above) which has similarly simple, ovate-lanceolate leaves, showing that in the field TRIANA considered the simple leaves and the finely divided leaves as belonging to the same species. More recently, further material has come from Colombia (*Herbert H. Smith* 1980, San Lorenzo ridges, Santa Marta, in Herb. Field Mus., Herb. New York Bot. Gard., etc.) which shows many leaves like those of the type of *B. crithmifolia*, but with leaf divisions narrower. A range of leaf outlines thus is shown that seems unbelievable, easily entitling *B. crithmifolia* to rank in this respect with such species as *B. heterophylla* Ort.

BIDENS HIRTELLA H.B.K. Nov. Gen. **4**:232. 1820.—*Bidens procumbens* H.B.K. *loc. cit.*

The type of *B. procumbens* (in Herb. Mus. Hist. Nat. Paris) differs only in the slightest way from that of *B. hirtella* (*ibid.*). KUNTH (H.B.K. *loc. cit.*) admitted the two forms to be very close. Had he possessed the wide range of data concerning variations in the related species of *Bidens* that, during the century since then, have steadily accumulated, he would not have hesitated to treat these as specifically the same.

**Bidens chrysanthemifolia** (H.B.K.), comb. nov.—*Cosmos chrysanthemifolia* H.B.K. Nov. Gen. **4**:239. 1820; *Cosmea chrysanthemifolia* Sprengel, Syst. Veg. ed. 16[III]. 615. 1826; *Cosmos*

[6] It is interesting to note that the mature head on the type of *B. delphinifolia* has at least one achene that is positively 2-aristate, showing no indication of a third awn ever having been present (cf. H.B.K. *loc. cit.*, "triaristata").

*chrysanthemoides* DC. Prodr. **5**:607. 1836; *Bidens Kunthii* Schz. Bip. Seem. Bot. Voy. Herald 308. 1852–1857; *Bidens parvulifolia* E. E. Sherff, BOT. GAZ. **56**:490. 1913.

This species was stated definitely by DECANDOLLE (*loc. cit.*) to come from Mexico, but KUNTH (H.B.K. *loc. cit.*) himself was uncertain as to its native country. DECANDOLLE, moreover, commented upon the closer affinity of the achenes with those of *Bidens* than with those of *Cosmos*. Whether he altered the specific name, however, through intent or through error, I am unable to say. But later, SCHULTZ BIPONTINUS (SEEM. *loc. cit.*), who frankly declared his belief that *Cosmos* was not a valid genus, used this altered name in citing it as a basis for his *Bidens Kunthii*, a name that, according to the Vienna Code, cannot stand.

ASA GRAY (Proc. Amer. Acad. **19**:16. 1884) strongly suspected that this plant was merely *Bidens humilis* H.B.K. and suggested a reexamination of the type material. KUNTH (H.B.K. *loc. cit.*) had described the color of the rays as "violacea, basim versus sulphurea." This description is borne out, not only by the coloring in the plate cited (that is, in copies of KUNTH'S work having the plates colored, as in John Crerar Library, Chicago), but by the type specimen in Paris (Herb. Mus. Hist. Nat. Paris), clearly the one from which the plate was made. This specimen, though discolored as to its rays, shows at least that the proximal ends of the rays were colored differently from the remaining portions, which latter seem surely to have been some shade of red.

More recently, fine material has been collected in Guatemala (*Heyde* and *Lux* 6173, alt. 900 m., Fraijanes, Dept. Amatitlan, September 1893, in Herb. Univ. of Chicago and in Herb. Kew), which belongs here. Singularly enough, it had been determined by JOHN DONNELL SMITH as *Bidens humilis* (cf. Gray *loc. cit.*), but the roseate rays and more or less *Cosmos*-like aspect are very distinct. The color of the rays in the dry condition varies from a pronounced roseate to a faded yellowish color, rather than showing a distinct sulphureous color definitely located toward the base as described by KUNTH. Still further material from the same small district in Guatemala (*W. A. Kellerman* 6112, alt. about 2500 m., Vol. Pacaya, Dept. Amatitlan, January 6, 1907, in Herb. Field Mus.) has been collected and fortunately is in a more mature condition. The

mature achenes match the ovary figured by KUNTH and show that there is not the slightest tendency to become rostrate as in *Cosmos*.

An examination of the original description of *Bidens parvulifolia* (Sherff, *loc. cit.*) shows that the second cited specimen (which I had seen in the U.S. Nat. Herb.) was obtained by the same collectors at the same altitude, time, and locality as was *Heyde* and *Lux* 6173 (see foregoing). The dried ligules were yellowish, the leaves were pubescent, and all but the top pair were simple. Since then, however, I have found other specimens (*Heyde* and *Lux* 6162 and 6163) showing numerous intergradations between the simple, pubescent leaves and the compound, mainly glabrous leaves; also, variations to a roseate color are shown in the rays. Thus *Bidens parvulifolia*, incredible as it will seem to any botanist who does not have at hand the intermediate specimens, must be interpreted as merely a form of *Bidens chrysanthemifolia* having minute, mainly undivided leaves.

BIDENS CERNUA L. Sp. Plant. 832. 1753.[7]—*Bidens gracilenta* Greene, Pittonia **4**:255. 1901; *Bidens prionophylla* Greene, *loc. cit.* 256; *Bidens glaucescens* Greene, *loc. cit.* 258; *Bidens lonchophylla* Greene, *loc. cit.* 258; *Bidens Macounii* Greene, *loc. cit.* 259; *Bidens leptopoda* Greene, *loc. cit.* 260; *Bidens marginata* Greene, *loc. cit.* 262.

In 1901, GREENE (*loc. cit.*) described a number of new species of *Bidens*. On examination of his types (mostly in U.S. Nat. Herb.) and cotypes (mostly in Herb. Gray and in Herb. Field Mus.) nearly three years ago, I was dismayed to find that most of these species represented what ordinarily had been regarded as mere ecological forms of *Bidens cernua* and *B. laevis*. Direct conversation with Dr. GREENE himself showed that back of his viewpoint regarding *B. cernua* (Greene *loc. cit.* 251–253) was the absolute conviction that the American specimens were native to America, and, being so, were hence specifically different from European specimens.[8] However, personal field study for the past four autumns, combined

[7] Here, as elsewhere in this series of articles, only the most relevant synonyms are cited, the others being left for a complete monographic treatment later.

[8] In emphasizing his views upon this subject, Dr. GREENE exclaimed: "I defy you to find a single species of Compositae that is native both to Europe and to North America." It is not my intention to discuss this opinion here, since it is quoted merely to show his viewpoint. I do desire, however, to acknowledge with gratitude the courtesies shown me by Dr. GREENE from time to time. For over two years we had been making field observations for each other upon various species of *Bidens*, but his recent death brought this mutual aid to an abrupt end.

with a careful examination of a vast amount of *B. cernua* material from different American and European stations, has convinced me only the more of the utter impossibility of separating the many forms as species. Scarcely a form occurs in the United States that is not duplicated by a precisely similar form in Europe. Even GREENE himself (*loc. cit.* 252) was compelled to declare "after careful and repeated comparisons made between European and American specimens of so-called *B. cernua*, I acknowledge inability to detect any strong technical characters upon which to separate them."

Again, in a single colony of *B. cernua*, frequently three or more dissimilar forms occur, with numerous intergradations. Thus in a single small colony north of Elgin, Illinois, many plants were diminutive, matching *B. minima* Huds.; some were tall and robust, matching *B. leptopoda* Greene (the type of which Professor J. M. MACOUN of the Canadian Geol. Surv. Herb. at Ottawa kindly permitted me to examine); and some were small plants grown from the rooting nodes of tall plants trampled down by cattle, and were practically identical with *B. marginata* Greene. In the same way, several of GREENE'S types are found on comparison with their cotypes in other herbaria to be merely slight variants from the standard form. In several of these cases, GREENE'S description was much too narrow to fit even the few cotypes examined.

BIDENS AMPLISSIMA Greene, Pittonia **4**:268. 1901.

This species has been discussed already (Sherff, BOT. GAZ. **59**: 312. 1915). The name *Bidens elata* then proposed as a substitute has since been found, however, at variance with an example cited in the Vienna Code for a similar case. Hence *B. elata* cannot be retained as technically the valid name.

BIDENS LAEVIS (L.) B.S.P. Prelim. Cat. N.Y. 29. 1888.—*Helianthus laevis* L. Sp. Plant. 906. 1753; *Helianthus foliis lanceolatis serratis laevibus* Gronov. Fl. Virg. **1**:104. 1739;[9] *Bidens chrysanthemoides* Michx. Fl. Bor. Amer. **2**:136. 1803; *Bidens helianthoides* H.B.K. Nov. Gen. **4**:230. 1820; *Bidens elegans* Greene,

[9] I could not find CLAYTON'S no. 195 among the Gronovian plants at the British Museum, and am unable personally to confirm this citation except from GRONOVIUS' description. But, in 1869, ASA GRAY (so Miss MARY A. DAY of Gray Herbarium has kindly ascertained for me) worked upon the Gronovian plants of the British Museum and listed CLAYTON'S no. 195 as "195 *Bidens chrysanthemoides!* (not *Heliopsis laevis*)."

Pittonia **4**:254. 1901; *Bidens lugens* Greene, *loc. cit.*; *Bidens formosa* Greene, *loc. cit.* 264; *Bidens Parryi* Greene, *loc. cit.* 265; *Bidens persicae-folia* Greene, *loc. cit.* 266.

The types of *Bidens chrysanthemoides* Michx. and *B. helianthoides* H.B.K. (both in Herb. Mus. Hist. Nat. Paris) appear precisely the same. The original description of both species shows their achenes to have been 2-aristate in each case, although many specimens have since been gathered showing the achenes often 3 or 4-aristate. A study of numerous specimens from the United States and Mexico seems to indicate a slight tendency for the western specimens to be more often 2-aristate, the eastern ones more often 3 or 4-aristate. But the variations are so abundant as to defy all attempts at delimiting the separate forms or races in a specific way (cf. TORR. and GR. Fl. N. Amer. **2**:353. 1842).

GREENE cites a single sheet for *B. formosa*, a plant from Delaware County, Pennsylvania. But in the Field Museum are 5 sheets of material (all by *J. K. Small*, Wetzel's Swamp, N. Harrisburg, September 1887) from the same state, and these show all gradations between *B. formosa* and *B. laevis*. Again, GREENE terms his *B. Parryi* an unwelcome species, "as uniting the habit of *B. cernua* and the fruit of the Platycarpaea group of species." But even if *B. Parryi* were a valid species, it would not be the first species to do this; for all the material of *B. laevis* that has flat, biaristate achenes does the same; and, moreover, *B. radiata* Thuill. (*B. platycephala* Oerst.) had long been noted as a species that likewise united *B. cernua* with *B. tripartita*, the latter a principal species of the Platycarpaea group (cf. G. SCHWEINFURTH, Verhand. Bot. Verein Prov. Brand. **2**:145. 1861). Indeed, GREENE himself, on another occasion (*loc. cit.* 261) had been led to consider *B. radiata* in this same connection, having suspected his *B. leptopoda* as being this species. DECANDOLLE, in monographing the genus *Bidens* (Prodr. **5**:594. 1836), defined the subgeneric section *Platycarpaea* with the evident purpose of admitting just such species as *B. cernua*, and actually classed *B. cernua* among the *Platycarpaea*.

Hence GRAY saw this plant and determined it personally. As his knowledge of this species was very keen, there is no question as to his accuracy. LINNAEUS' private specimen of *Helianthus laevis* L. (in Herb. Linn.) is *Heliopsis* (cf. GRAY, Synopt. Fl. $1^{11}$:255. 1884; also PERSOON, Synops. Plant. **2**:473. 1807).

Several other species described by GREENE and based upon characters seemingly inconsistent or difficult at present to evaluate, are reserved for later treatment.

UNIVERSITY OF CHICAGO

## EXPLANATION OF PLATE XXXI

*Bidens mirabilis.*—*a*, spray ×0.7; *b*, exterior bract ×4; *c*, interior bract ×4; *d*, palea ×4; *e*, floret ×7; *f*, anther ×35; *g*, pollen grain ×350; *h*, achene ×11; *i*, portion of leaflet ×3; all from type in Herb. Kew.

SHERFF on BIDENS

# THE OCCURRENCE OF BACTERIA IN FROZEN SOIL

E. C. HARDER

(WITH TWO GRAPHS)

## Introduction

The results of various investigators, notably CONN and BROWN, have shown that the actual number of bacteria in the soil often increases with a decrease in temperature. This phenomenon is not confined to a gain in the number of bacteria alone, but is accompanied by a stimulation of the activity of the microorganisms. Many bacteriological processes, as ammonification, denitrification, and free nitrogen fixation, have shown an increase in frozen soils.

Because of the practical importance of this problem for agricultural practice it was thought advisable to note the effect of cold and moisture on the number of bacteria in Madison soil. Here the variations in temperature are greater than those recorded by former investigators.

In order to study what effect these great variations would exert on the number of bacteria, a series of plate counts was made. If the number of bacteria in the soil increases with freezing, there should be a parallel increase in available plant food. Many questions arise. Do all soils when sampled in the winter show the same general increase? What effect does stimulation of bacteria have on soil fertility? It has been noted that an increase in bacterial activity results in an increase in food for higher plants. The increase in the number of bacteria during the winter probably plays an important part in soil fertility. This is decidedly at variance with the earlier idea that frozen soils are dormant.

## Previous work

The more recent experiments on the activity of bacteria in frozen soil were conducted by CONN[1] and BROWN and SMITH.[2]

[1] CONN, H. J., Bacteria in frozen soil. I and II. Centralbl. Bakt. **28**:422–434. 1910; **32**:70–97. 1911.

———, Bacteria of frozen soil. N.Y. Agric. Exp. Sta. Tech. Bull. 35. July 1914.

[2] BROWN, P. E., and SMITH, R. E., Bacterial activities in frozen soils. Agric. Exp. Sta. Iowa State College of Agric. Research Bull. 4. January 1912.

CONN's experiments dealt mainly with the number of bacteria in frozen soils, which he compared with the number in the same soils when in an unfrozen condition. He worked both with field and with potted soils and reached the following conclusions: (1) "the increase in number of bacteria after freezing is not due to the increase in soil moisture which usually occurs in winter"; (2) "the same increase in germ content may take place in potted soil, where there is no possibility that the bacteria are carried up mechanically from lower depths during the process of freezing"; and (3) this phenomenon is probably "due to an actual growth of bacteria after the soil is frozen."

The experiments were performed with the samples of field soil taken from plates prepared for the purpose, both aerated and unaerated soils being examined. Each type of soil, therefore, probably had a nearly uniform bacterial content originally throughout its mass, and the changes that occurred in it from time to time must be ascribed to the effect upon it of changes in the atmosphere. Unfortunately, samples were taken only at irregular intervals, so that, while the results show a general higher content of bacteria in frozen soils during the winter, they are not sufficiently detailed to show definitely when such increases occurred and to what they were due.

It is suggested that possibly freezing may have the effect of breaking up compact colonies which under ordinary conditions would not separate into individuals, thus making the increase only an apparent one, owing to more individuals producing separate colonies on the plates. This view is discarded, however, because upon the thawing of the soil the number of bacteria again decreases to practically what it was before freezing. It is claimed also that the maximum number is reached several weeks after a frost.

CONN concluded, therefore, that the increase is due to actual multiplication, and the supposition is that such multiplication takes place in certain denser portions of the soil solution, which, as suggested by BROWN and SMITH (*loc. cit.*), probably do not freeze. It is suggested that conditions in these unfrozen portions may favor the growth of certain prolific kinds of bacteria and suppress

the growth of other varieties which at ordinary temperatures interfere with the growth of these prolific kinds.

An analogous hypothesis proposed by RUSSELL[3] for increases in the number of bacteria after partial sterilization by heat, frost, or other means is that by such partial sterilization the protozoa are killed, thus permitting the unhindered development of bacteria which under ordinary conditions is held in check by protozoa.

BROWN and SMITH (*loc. cit.*) in their investigations dealt mainly with the physiological activities of bacteria under conditions of low temperature and frost, although they also made some determinations of the number of bacteria in frozen soil. Their principal conclusions regarding the ammonifying, nitrifying, denitrifying, and nitrogen fixing powers of frozen soils are as follows: (1) that "frozen soils possess a much greater ammonifying power than unfrozen soils"; (2) that "during the fall season, the ammonifying power of the soil increases until the temperature of the soil almost reaches zero, when a decrease occurs, and this is followed by a gradual increase and the ammonifying power of the soil reaches a maximum at the end of the frozen period"; (3) that "the nitrifying power of frozen soils is weak and shows no tendency to increase with extension of the frozen period"; (4) that "frozen soils possess a decided denitrifying power which seems to diminish with the continuance of the frozen period"; (5) that "during the fall season, the denitrifying power of the soil increases until the soil freezes, after which a decrease occurs"; (6) that "frozen soils possess a nitrogen fixing power which increases with the continuance of the frozen period, being independent of moderate changes in the moisture conditions, but restricted by large decreases in moisture"; and (7) that "in the fall, the nitrogen fixing power of the soil increases until the soil becomes frozen, when it almost ceases, after which a smaller nitrogen fixing power is established."

The experiments on which these conclusions are based were conducted with air-dried soil of uniform texture and composition as a medium. This soil was enriched with suitable materials for ammonification, nitrification, denitrification, or nitrogen fixation.

[3] RUSSELL, E. J., The effect of partial sterilization of soil on the production of plant food. Jour. Agric. Sci. 5:152–221. 1913.

One-hundred gm. samples of soil thus prepared were then inoculated with infusions consisting of a mixture of the fresh soils to be tested and sterile water, 10 cc. of the infusion (containing in each case about 5 gm. soil) being added to each 100 gm. sample. The final moisture content of the soils during incubation was 20 per cent.

BROWN and SMITH assert that actual multiplication in the numbers of bacteria takes place in frozen soils, and that to this must be ascribed the increased numbers during the winter months. They present the hypothesis that, owing to the concentration of various salts in the film of hygroscopic water around soil particles, this film probably does not freeze under ordinary winter conditions, and bacteria may live and multiply in it.

## Present investigations

SUMMARY OF RESULTS.—During the winter of 1914–1915, the writer conducted a series of experiments with field and potted soils. The results obtained justify conclusions which are somewhat at variance with those obtained during the recent investigations by CONN at Ithaca and Geneva, New York, and by BROWN and SMITH at Ames, Iowa; and it seems advisable, therefore, to publish them. The principal results obtained were as follows:

1. It was found that the number of bacteria in surface soil increased markedly after heavy frosts and in general maintained a high average during the winter months. The increases and decreases, however, were found to bear a distinct relation to the moisture content.

2. The potted soils failed to show such marked increase in bacterial content after frosts. On the contrary, the enriched cultures showed a distinct retardation of bacterial growth when in a frozen condition.

3. The bacterial flora was more or less the same during the fall, winter, and spring, with the exception that after heavy frosts the small transparent colonies characteristic of water and of deeper soils formed a larger proportion of the growth on the plates.

From these results it seems reasonable to conclude that ordinary soil bacteria undoubtedly withstand cold to a marked degree, even to temperatures as low as 4° C. or more below zero. The increase

in numbers, however, seems to be due to mechanical transportation by moisture coming up from below during heavy frost, and where such transportation is not possible there is an actual retardation in growth as compared with that in unfrozen soils.

EXPERIMENTS WITH FIELD SOIL.—The investigations were begun during the latter part of October, and the samples were examined every week until the latter part of February, after which time the samples were examined at greater intervals.

A dark, medium rich, slightly sandy garden soil was studied. It was obtained from the university campus near the College of Agriculture, and care was taken to secure successive samples from exactly the same place. The soil was sampled to a depth of about 6 inches each time, thus giving an average of a surface layer to this depth. The temperature of the soil was taken roughly with an ordinary thermometer.

The entire sample was thawed, when necessary, and thoroughly mixed in a mortar, previously washed out with 95 per cent of alcohol. Twenty gms. of soil were then mixed with 400 cc. of sterile water, and from this 25 cc. were carried to a second 400 cc. sterile water blank, and so on to the fourth dilution. From the fourth or fifth dilution plates were poured and these were counted after an incubation period of 8 days at 28° C. Heyden Nährstoff agar was used as a culture medium.

It appears that in order to obtain conclusive results regarding the bacterial content of soils, samples should be investigated at short intervals of time, perhaps every few days, or even every day, as at times of heavy frost, or after rainfall. It was found that the bacterial content of soils is closely dependent on atmospheric conditions as regards temperature and precipitation. When atmospheric conditions vary rapidly the bacterial content of soils also may change rapidly. Table I shows the variations in the bacterial content of the soil from October 1914 to April 1915.

Table I shows the general close relation between the moisture content and the number of bacteria in the soil. This is also shown in graph 1. While slight discrepancies undoubtedly occur, the general correspondence is very marked. Graph 2 gives the curves of high and low daily temperature, as well as figures for the

precipitation during the period that the experiments were carried on.

It will be seen by an examination of table I that there was some variation in the bacterial content during the latter part of October

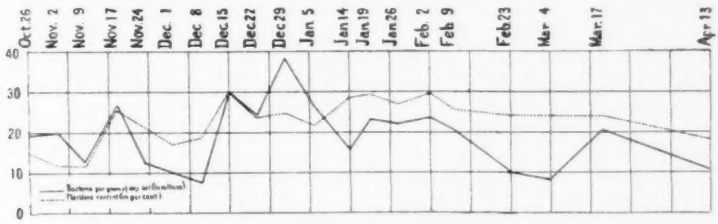
TABLE I

| Date | Percentage of moisture content of soil | Temperature of soil | Average number of colonies per plate* | Bacteria per gm. dry soil | Remarks |
|---|---|---|---|---|---|
| 1914 | | | | | |
| October 26 | 15.02 | ..... | 168 | 19,420,800 | Soil unfrozen |
| November 2 | 11.83 | ..... | 182 | 20,187,358 | Soil unfrozen |
| 9 | 11.79 | ..... | 114 | 12,692,786 | Soil unfrozen |
| 17 | 25.64 | −0.5C. | 203 | 26,824,623 | Soil frozen 4–5 inches |
| 24 | 20.98 | 0.0 | 100 | 12,434,800 | Upper 1 inch thawed; below frozen |
| December 1 | 17.02 | +8.0 | 81 | 9,534,105 | Soil completely thawed |
| 8 | 18.44 | +1.0 | 62 | 7,469,450 | Rain December 7 Frost December 9 |
| 15 | 30.05 | −3.0 | 212 | 29,781,548 | Heavy frost December 13 |
| 22 | 23.48 | −4.0 | 188 | 24,018,316 | Snowfall December 20; continued frost |
| 29 | 24.48 | −0.7 | 293 | 38,122,523 | Heavy frost December 25–26; heavy snowfall December 29 |
| 1915 | | | | | |
| January 5 | 21.52 | −1.0 | 213 | 26,668,230 | Mild temperature |
| 14 | 28.62 | −1.0 | 115 | 15,830,555 | Mild temperature |
| 19 | 20.24 | −3.0 | 166 | 23,051,258 | Thaw and subsequent frost |
| 26 | 26.87 | −2.7 | 164 | 22,035,532 | Cold weather January 21–24 |
| February 3 | 29.53 | −1.0 | 168 | 23,425,080 | Very severe frost January 27–28 |
| 9 | 25.60 | −3.0 | 153 | 20,206,710 | Thaw and rain February 4–5 |
| 23 | 24.03 | +1.0 | 76 | 9,824,216 | Soil completely thawed |
| March 4 | 24.10 | −0.7 | 65 | 7,993,570 | Upper 3 inches frozen |
| 17 | 24.00 | +0.5 | 157 | 20,298,373 | Upper ½ inch frozen |
| April 13 | 18.40 | +4.0 | 89 | 10,717,113 | Completely thawed |

* Fourth dilution

and the first part of November, while the soil was still unfrozen. This variation seems to have been independent of the moisture content. On November 17, some days after the first frost, a distinct increase in the number of bacteria was shown, accompanied by a great increase in moisture. During the subsequent period of mild

weather continuing to December 9, the bacterial content of the soil gradually decreased to much below the original amount, the lowest count of the winter, 7,459,450 bacteria per gm. of dry soil, occurring during this period. At the same time the soil thawed and the moisture content decreased. The count of December 15, taken some days after the second frost, again showed a marked increase in bacterial numbers, as well as in moisture content. Following this there was a continuous cold period culminating in very heavy frost from December 25 to 27. On December 29, following this heavy frost, we had the highest bacterial count of the winter, 38,122,523 bacteria per gm. of dry soil. The next count, January 5, showed a considerable decrease with but a slight decrease in moisture content. This is probably to be explained

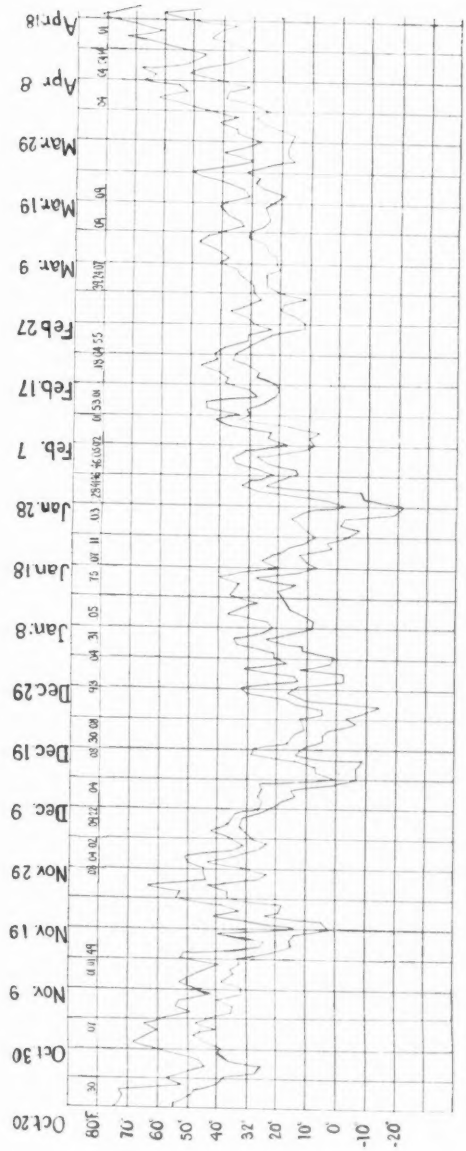



GRAPH 1.—Curves showing the bacterial and moisture contents of Madison soil from October 26, 1914, to April 13, 1915.

by the fact that the high count of December 29 included many forms that could not withstand the more severe cold to which they were exposed in the upper soil layer. The low count of January 14 accompanied by an increase in moisture is difficult to explain.

After this date there was no great variation in the bacterial content until February 23, when there occurred a marked decrease accompanying the complete thawing of the soil. During this thawing, however, there was only a slight decrease in soil moisture. The figure for April 13 shows the normal bacterial content of the soil during the spring.

EXPERIMENTS WITH POTTED SOIL.—In order to determine whether the high bacterial content of frozen soil was due to an actual increase in growth, or whether other factors brought about this phenomenon, two duplicate sets of potted soil were prepared.




GRAPH 2.—Curves showing high and low daily temperatures at Madison, Wisconsin, and figures giving precipitation from October 20, 1914, to April 20, 1915.

One set was kept at room temperature and the other set was placed outside, subject to atmospheric temperatures.

Six jars (3 for each set) of glazed earthenware, holding about 1850–1900 gm. of soil, were used. These were filled with soil prepared as follows: nos. 1 and 2, Miami silt loam containing 23 per cent moisture; nos. 3 and 4, Miami silt loam containing 23 per cent moisture and 1 per cent dextrose; and nos. 5 and 6, Miami silt loam containing 28 per cent moisture.

The soil was thoroughly mixed and the moisture raised to the proper amount, care being taken to secure a uniform moisture content throughout the sample. Muslin was tied over the tops of the jars, which allowed free access of air but which excluded dust. Jars 2, 4, and 6 then were placed outside of a window, and protected from rain and snow by a large bell jar which allowed free circulation of the air. Jars 1, 3, and 5 were kept in a room at an average temperature of about 25° C. The jars were left untouched for a period of 18 days (February 16–March 6). The average daily temperatures for this period which affected the outside jars are shown in graph 2.

At the end of the period an average 20 gm. sample was taken from each of the jars and treated in the same way as the field soil samples previously described. Plates poured with Heyden Nährstoff agar and counted after 8 days gave the results indicated in table II.

TABLE II

| No. of jar | Treatment | Percentage of moisture content of soil | Average number of colonies per plate* | Bacteria per gm. dry soil |
|---|---|---|---|---|
| 1 | 23 per cent $H_2O$ | 8.42 | 51 | 5,471,004 |
| 2 | 23 per cent $H_2O$ (frozen) | 15.00 | 48 | 5,548,800 |
| 3 | 23 per cent $H_2O$ 1 per cent dextrose | 9.09 | 261 | 28,491,543 |
| 4 | 23 per cent $H_2O$ 1 per cent dextrose (frozen) | 15.80 | 155 | 18,089,275 |
| 5 | 28 per cent $H_2O$ | 9.31 | 61 | 6,009,107 |
| 6 | 28 per cent $H_2O$ (frozen) | 17.48 | 51 | 6,073,131 |

*Fourth dilution.

It should be noted that in the cases where the soil was kept in the room, the evaporation was much more rapid than in the soils

kept outside, so that while the original moisture content was the same, when the counts were made the amount of moisture present in the jars kept outside was nearly double that in the jars kept in the room.

The results recorded in table II show clearly the retardation in growth which was caused by cold and frost. In the case of jars nos. 1 and 2, the number of bacteria per gm. of soil is almost the same in the two samples, yet sample no. 2 has only slightly less than twice as much moisture as sample no. 1. Jars nos. 3 and 4 show the retardation even better. Here 1 per cent of dextrose was added so as to produce a rapid growth. No. 3 with a much lower moisture content than no. 4 shows a much greater increase in growth. This is the reverse of what might be expected to happen under ordinary conditions, and must be ascribed to the action of frost, since normally the bacterial content should rise with an increase in moisture. Jars nos. 5 and 6 gave results similar to jars nos. 1 and 2, the number of bacteria being slightly higher because of the higher moisture content.

In general these figures show that even a much higher moisture content was not sufficient to counteract the retarding in growth due to cold.

### Types of bacteria in frozen soil

No detailed study of the varieties of bacteria in the soil was made, since this would have required much more time than was at the writer's disposal. Nevertheless, general differences in the kinds of colonies present in successive counts were noticed.

Usually the plates contained a varying number of raised colonies of yellow, red, and fluffy white actinomycetes, a few spreaders of the *B. mycoides* type, some red or yellow chromogens, numerous small, slow-growing, transparent colonies, and many white or cream colored colonies without distinctive marks, some of them raised and others flat. Occasionally the plates showed a few opalescent colonies.

So far as could be noticed from the examination of colony growths, there was no distinct difference between the fall, winter, and spring floras. It was noticeable, however, that the relative

proportions of the different types sometimes changed markedly in successive counts. Thus it was found that after heavy frosts the small transparent colonies made up sometimes one-half or more of the total number of colonies on the plates. In subsequent counts they would gradually decrease in number.

The actinomycetes and the spreaders did not seem to be affected by the frost, being present on nearly every plate counted during the winter. The chromogens were more irregular in their occurrence and apparently were somewhat less abundant during very cold periods.

The writer wishes to express his indebtedness to Professor E. B. FRED, University of Wisconsin, for helpful suggestions and criticisms.

UNIVERSITY OF WISCONSIN
MADISON, WIS.

# THE PROTHALLIA OF OPHIOGLOSSUM VULGATUM

NORMA E. PFEIFFER

(WITH FOUR FIGURES)

The gametophyte of *Ophioglossum* was found first by METTENIUS in material of *O. pedunculosum* Desv. in the botanical gardens at Leipzig, in 1856. Almost 50 years later, LANG collected prothallia of *O. pendulum* in Ceylon, in the Barrawa Forest Reserve. These were found to be developed in the humus between leaf bases of an epiphytic *Polypodium*, and, as in the case of METTENIUS, were found growing spontaneously, but were not developed in cultures from the spores. Later, CAMPBELL found similar prothallia in humus collected between leaves of *Asplenium nidus* in Java. In 1906 he also collected prothallia of *O. molluccanum* at Buitenzorg. In 1904, BRUCHMANN reported the finding of gametophytes of *O. vulgatum* in nature. He worked over a considerable period of time, free days from May to October, in isolating about 70 young prothallia, besides those with sporophytes, in a particularly favorable region in the Thuringian Forest. The area concerned was a depression surrounded by ash trees and alders. The occurrence of so many specimens was attributed partly to the protection against wind currents which might carry the spores away, although the depression was subject to overflows from rains, which might remove the spores also. CAMPBELL considers the latter of importance because of the possible effect of submergence upon germination of spores. It would seem likely that this process is favored by inundation. BRUCHMANN obtained the prothallia by arduous labor, working over the soil between the mature plants. That the prothallia are not numerous is evidenced by the small return of two prothallia per working day.

The situation in which the present growth of *O. vulgatum* occurs is practically the low prairie type previously described for *Thismia americana*.[1] The plants of *Ophioglossum* occur among the

[1] PFEIFFER, NORMA E., Morphology of *Thismia americana*. BOT. GAZ. **57**:122–135. *pls. 7–11*. 1914.

prairie plants. Spots have been burned, and here the plants show very distinctly, owing to a partial elimination of the grasses and other plants which ordinarily tend to obscure the smaller *Ophioglossum* plants. Where there is much shade, *Selaginella apus* and *Aneura pinguis* occur, as in the *Thismia* patch, which is close at hand. The habitat is evidently low and wet, inundated in spring. Early in July, *Riccia fluitans* in small amounts was also found, and late in July 1915, after a rather wet month, some of the field was under water. There were, however, hummocks as well as more extensive little plots not submerged. Compared with the other situation in the Chicago region where *O. vulgatum* has been found, that is, near Gary, the present station in the southeast outskirts of Chicago seems wetter. The difference noted in the time of maturity of fertile spikes in the two areas is probably related to the difference in situation. In the moister place, some spikes were still unshed on July 24, whereas the spikes were already gone in the drier, less protected Gary situation, on July 15. Working on CAMPBELL'S theory that inundation favors spore germination, one may suppose that

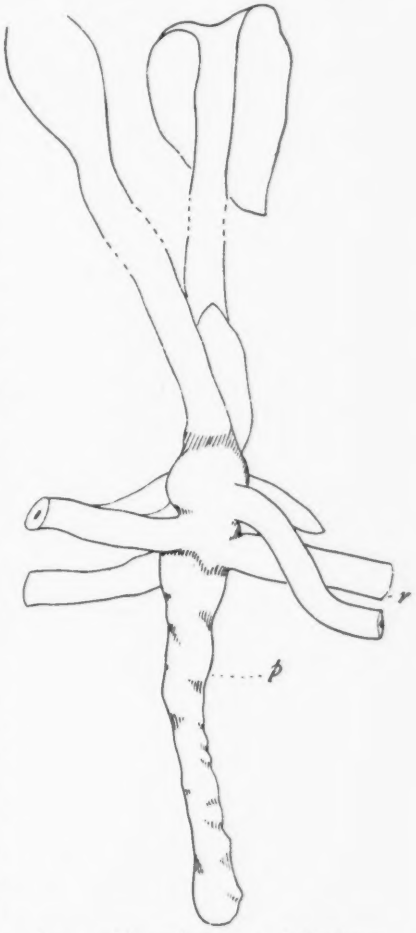



FIG. 1.—Old prothallium of *Ophioglossum vulgatum* with well developed sporophyte; *p*, prothallium; ×3½.

this difference would account for the finding of any prothallia here, whereas their occurrence in the Gary area has not been noted.

The gametophytes so far found have had attached sporophytes, either well developed

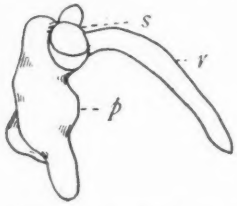



FIG. 2.—Prothallium with younger sporophyte; *s*, sporophyte base; *r*, first root; *p*, prothallium; ×33⅓.

or very young. With more time at one's disposal, there is little doubt that younger prothallia could be found. Quite evidently, from the age of the sporophyte, the gametophytes remain attached for some seasons after fertilization has occurred. There remains to be done the mechanical labor of sorting until younger and younger material is obtained.

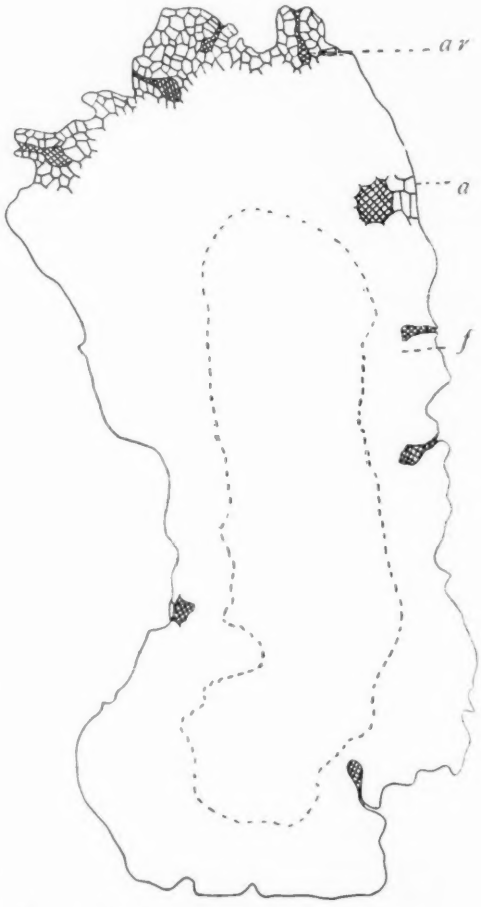



FIG. 3.—Longitudinal section of prothallium; *a*, antheridium; *ar*, archegonium; *f*, fungus-infected region; ×33.

The appearance of prothallia is entirely similar to that described by BRUCHMANN. Most of them are simple (figs. 1 and 2), although branching

occurs. In external appearance the prothallium may be distinguished readily from roots by the irregular form and uneven surface it exhibits owing to the sex organs, as compared with the straight and very smooth roots or rhizomes. The end is more or less round or even tuberous, as indicated in BRUCHMANN'S figures, as compared with the pointed root tip. Usually in specimens with well developed sporophytes, the decided brown coloring of the prothallium is another distinguishing character, although here it is often difficult to distinguish sharply between the base of the sporophyte and the gametophyte. The younger material, as well as the growing region of older gametophytes, is lighter in color, however. As compared with the horizontal position of most of the roots, the prothallium is usually oriented with its long axis nearly vertical.

FIG. 4.—Section of prothallium showing young antheridia (*a*); × 33.

Sections of a prothallium with a young sporophyte attached show the surface to be well dotted with sex organs (fig. 3), as may be seen even in bulk material by use of a hand lens. The necks of old archegonia are conspicuous, as are the positions of antheridia. Occasionally there are antheridia still unshed, as shown on a small excrescence near the upper portion, where fungal hyphae had not yet entered (fig. 4). Here it is probable that there was continued production of sex organs after fertilization. Sufficient material for working through developmental stages was not at hand, but the stages found confirm BRUCHMANN'S conclusions regarding the sex organs.

The general topography does not differ from that figured by BRUCHMANN, except that there is usually only one cortical layer free from fungi. Within this is the region, 4–6 layers of cells deep, in which the fungus is conspicuous, and then the central region, staining more lightly because of the absence of mycelium in the

cells. This region contains more or less reserve food in the form of starch grains.

There is little doubt that reproduction by vegetative spread is by far the more common method, but scattered among plants so produced are the far less numerous specimens arising after gametophyte production has occurred.

UNIVERSITY OF NORTH DAKOTA
GRAND FORKS, N.D.

# THE MEASUREMENT OF OXIDATION POTENTIAL AND ITS SIGNIFICANCE IN THE STUDY OF OXIDASES

G. B. Reed

(WITH TWO FIGURES)

In the course of a series of investigations on the rôle of plant oxidases, the writer has found it necessary to follow with accuracy the progress of various oxidation reactions. The best method of accomplishing this is found undoubtedly in the measurement of the oxidation potential of the solutions entering into the reactions. Since this method has never been employed in the study of biological processes, and has only a limited use in physical chemistry, a description of the apparatus as modified by the writer may be of interest.

According to electro-chemical conceptions, oxidation is the process of taking on positive charges of electricity or the giving up of negative charges of electricity. Hence if we have a measure of the tendency of a substance to take on or give up electrical charges, we may determine the oxidizability of that substance.

If we consider a hydrogen electrode, that is, a strip of indifferent metal, such as platinum, platinized to increase its surface and charged with hydrogen gas, dipping into a solution containing hydrogen ions, we see that there will be a potential difference between the electrode and the solution. The hydrogen on the electrode will give up to the solution positively charged hydrogen ions until equilibrium with osmotic pressure of the hydrogen ions in solution is reached. If two such electrodes dip into solutions containing hydrogen ions at different concentrations connected by a liquid (as through a siphon), the potential of the cell is equal to the algebraic sum of the two single potentials, and is expressed by the formula

$$E = \frac{RT}{2Q} ln \frac{P}{P_1},$$

where $P$ and $P_1$ represent the concentrations of hydrogen ions in solution.[1] If the concentration of hydrogen ions in one solution is known, the concentration of the second may be calculated from the observed potential. In practice it is customary to substitute a standard half-cell (for example, a calomel electrode) for one of the hydrogen electrodes.

In a similar manner, when an oxygen electrode dips into a solution, the oxygen on the electrode tends to give up to the solution negatively charged oxygen ions until equilibrium is reached. The electrode, therefore, becomes positively electrified. If there be added to the solution an oxidizing agent (which, by definition, gives up positive charges), it will increase the positive charge on the electrode. In the case of potassium permanganate in acid solutions, the source of the positive charge may be represented by the equation

$$MnO_4^- + 4H^+ = Mn^{++} + 4OH^- + 5+,$$

and the potential may be calculated from the formula[2]

$$E = \frac{RT}{5F} ln\, K \frac{(MnO_4^-) \times (H^+)^4}{(Mn^{++}) \times (OH^-)^4}.$$

Experimental complications are met with in using platinum as an electrode, since it appears that oxygen combines with platinum to form oxides.[3] These complications are of theoretical interest, but for practical purposes they may be neglected, since the platinum electrode, when charged with oxygen, gives satisfactory comparative values of the oxidizing and reducing ability of different compounds. This is true even when the manner in which the compound ionizes is not known.

The measurements recorded in this paper, and in investigations to be reported on later, were made with the apparatus illustrated by fig. 1. The reaction cell $A$ consisted of a 200 cc. beaker containing the solution to be tested, into which the two electrodes dipped. The electrode $B$ was made from a platinum crucible of

[1] LEBLANC, M., Electro-chemistry; translation by WHITNEY and GOWAN. New York. 1907 (p. 195).

[2] CROTOGINO, F., Zeit. Anorg. Chem. **24**:225. 1902.

[3] SCHOCH, E. P., Jour. Phys. Chem. **14**:665. 1910.

about 50 cc. capacity, platinized on both sides in the ordinary manner, and completely submerged in the solution. The other half of the cell was a standard calomel electrode (*C*) made up in a 150 cc. bottle with saturated KCl. To prevent contamination by diffusion of the reaction mixture into the electrode, connection was made by means of a siphon to a bottle (*D*) containing saturated KCl; and from this, by means of a second siphon, connection was made with the reaction cell *A*. To further prevent diffusion, this

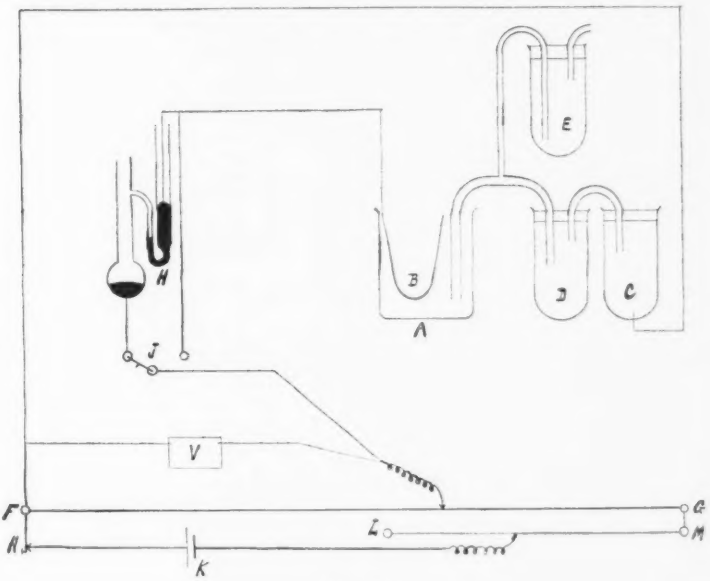



FIG. 1

second siphon contained a cotton wick for a part of its length, and was kept closed by means of a pinchcock (on a rubber section of the siphon), and finally terminated in a fine capillary which dipped into the reaction mixture. The reservoir of saturated KCl at *E* allowed the capillary to be washed out frequently without disturbing the electrode.

Measurement of the total potential of the cell (that is, the potential at the platinum electrode plus the known potential of the

calomel electrode as well as the exceedingly small contact potential between the KCl and the solution in *A*) was made by the Poggendorf compensation method, with the apparatus so arranged that the amount of current taken from the cell was reduced to a minimum.

The calomel electrode was connected with one end of a slide wire bridge (*FG*) and the platinum electrode was connected, through a zero instrument *H* with the sliding contact. A Lippman capillary electrometer (since it takes no current) was found more satisfactory as a zero instrument than a galvanometer, which is usually employed. To have the electrometer at zero at the beginning of a reading, it was kept short-circuited through itself by properly shifting the key *J*.

A potential was maintained along the wire *FG* by means of the battery *K* (3 dry cells in parallel). The variable resistance *LM* permitted this to be regulated to suit the requirements. By connecting a voltmeter *V* between the negative end of the bridge and the sliding contact, it is possible to read off the potential taken from the battery circuit at any time.[4]

In taking a reading, the battery circuit through the bridge was closed by the key *N*, and the circuit to be measured was immediately closed by the key *J*. The sliding contact was then adjusted so that the potential from the battery circuit was just sufficient to balance that produced in the reaction beaker *A*. When this condition was reached no current flowed and the electrometer was in equilibrium. The reading of the voltmeter then gave the potential of the cell.

The potential produced at the platinum electrode could then be determined by subtracting the positive single potential of the calomel electrode, usually referred to as 0.56 volt, from the total potential observed. For comparative purposes, however, since the potential of the calomel electrode was constant, the total potential of cell may often be used.

The curve of the oxidation of oxalic acid by acidified potassium permanganate, shown in fig. 2, illustrates the way in which a reaction may be followed by this method. On placing a platinized

[4] This use of a voltmeter, to avoid the use of a standard cell and potentiometer calculations, was suggested by HILDEBRANT, Jour. Amer. Chem. Soc. **35**:869. 1913, in connection with measurements of H ion concentration.

electrode, connected as previously described, in dilute oxalic acid, the potential quickly drops to very nearly the minimum value. The potential may continue to drop for some hours (this slow drop amounting to 0.1–0.2 volt) if the electrode has previously been subjected to an oxidizing agent; but if the electrode is previously subjected to a reducing agent, a constant potential is reached much more quickly. When standardized potassium permanganate (in this case 0.001 M) is added, the potential rises slowly until the concentration of positive ions becomes nearly equal to that of the negative ions, when a trace of permanganate causes a jump in the potential. The last trace of permanganate is sufficient to change the solution in contact with the electrode from a reducing agent to an oxidizing agent, that is, to one which gives up positive ions. It is evident that by this method the progress of an oxidation reaction may be followed with great accuracy.

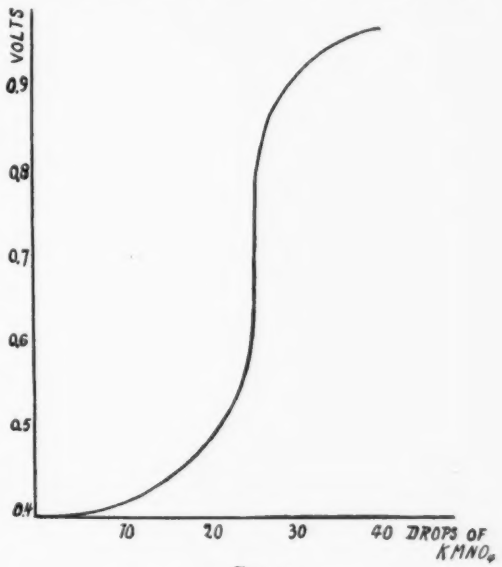



FIG. 2

The effect of a catalyzer in accelerating an oxidation reaction may be studied, in some cases at least, by this method with excellent results. The writer has begun some investigations of this character, in which various "inorganic ferments" have been used to catalyze the reaction with a view to utilizing the results in constructing a theory of oxidase action. These results will be described in subsequent papers.

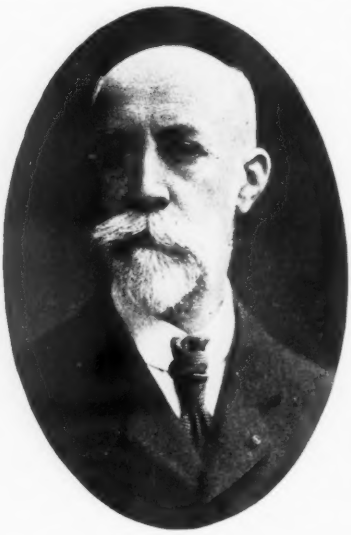
LABORATORY OF PLANT PHYSIOLOGY
HARVARD UNIVERSITY

# BRIEFER ARTICLES

## CHARLES RENÉ ZEILLER

(WITH PORTRAIT)

It is an interesting coincidence that November 1915 should have marked the passing of the most distinguished paleobotanists of the two warring nations, France and Germany. Each was a leader hard or impossible to replace, and each saw the light in the forties of the last century. To another has fallen the task of recording for American botanists the obituary of Count SOLMS-LAUBACH. The present notice deals with CHARLES RENÉ ZEILLER, a son of the lost province Lorraine. His early activities were as a member of the auxiliary corps of engineers in the Franco-Prussian war of 1870. On the scientific side he first busied himself with mineralogy and general geological work. Later he became more and more interested in paleobotany and in this connection is a high exemplification of the logical mind and catholicity of view which are the attributes of the Gallic race. Not only did he study many fossil floras of diverse geological ages and geographical occurrence and give many new names to science, but he likewise wrote with distinction concerning the climates and phytogeographical areas of the past, as well as of the anatomy and evolutionary history of the types which came under his notice. His stratigraphic accomplishments were of a high order of merit also, in a field where plants have been thought by many to have less value as indicators of geological time.



Under his fostering care the collection at the École des Mines in Paris became the most important and best equipped in Europe, with the possible exception of that presided over by NATHORST in Sweden, claiming the interest of the scientific visitor to Paris rather than that at the Museum in the Jardin des Plantes, which has fallen somewhat into decay since the death of RENAULT. This care for details, accompanied by the much rarer quality of the broad outlook, characterized ZEILLER as they do his nation. For a number of years he performed the laborious task of summarizing the literature and results of paleobotany for the *Révue Générale de Botanique*, and in the writer's opinion no better account of the subject, for the times it covers, has ever been written.

ZEILLER was a delightful correspondent, and his discriminating praise of work done was a strong incentive to a later and less inspired generation to persevere in a science which only now is beginning to claim its proper place. His *Éléments de Paléobotanique*, although professedly only a compendium of the subject, may without exaggeration be characterized as the broadest and best work on the subject yet written. We of the newer continent join with France in paying tribute to one of her distinguished sons "dead on the field of honor."—E. C. JEFFREY, *Harvard University*.

# CURRENT LITERATURE

## MINOR NOTICES

**Genetics.**—This is the title of a new journal published by the Princeton University Press, whose initial number appeared in January 1916. The subtitle is "A periodical record of investigations bearing on heredity and variation." The editorial board comprises W. E. CASTLE, E. G. CONKLIN, C. B. DAVENPORT, B. M. DAVIS, E. M. EAST, R. A. EMERSON, H. S. JENNINGS, T. H. MORGAN, RAYMOND PEARL, and G. H. SHULL, the last named being the managing editor. Such an array of prominent geneticists insures a journal of first order. It is to be issued bimonthly. An annual volume approximates 600 pages, the subscription price being $6.00. A most appropriate introduction is made by the publication of a hitherto unpublished portrait of MENDEL, being a photographic copy of an oil painting hanging in the parlor of the monastery at Brünn in which MENDEL was for 15 years the abbot. The three papers published are as follows: "Non-disjunction as proof of the chromosome theory of heredity," by CALVIN B. BRIDGES; "The numerical results of diverse systems of breeding," by H. S. JENNINGS; and "Hereditary anchylosis of the proximal phalangeal joints (symphalangism)," by HARVEY CUSHING.—J. M. C.

**Principles of plant culture.**—The eighth edition of GOFF's *Principles of plant culture*, revised by MOORE and JONES,[1] has just appeared. The first edition was issued in 1897, with the statement that the book "is intended especially for students who have had little or no previous instruction in botany." The book has stood the test of use by many teachers and students for over 20 years. The titles of the chapters indicate the kind of information the book offers: seed germination and the plantlet, the growing plant, the root and the soil, leaves and buds and flowers, the fruit and the seed, decline of growth and the rest period, unfavorable temperature, unfavorable light and wind, unfavorable food supply, animal parasites, vegetable parasites and weeds, propagation, plant breeding. With the growing interest in the rational handling of plants for practical purposes, this little volume should meet a growing need.—J. M. C.

**Plant teratology.**—WORSDELL[2] has published the first volume of a work intended to succeed MASTERS' well known *Vegetable teratology*, published by

[1] GOFF, E. S., The principles of plant culture. 8th ed. Revised by E. G. MOORE and L. R. JONES. 8vo. pp. xxiii+295. New York: Macmillan. 1916.

[2] WORSDELL, W. C., The principles of plant teratology. Vol. I. 8vo. pp. xxiv+270. *pls. 25. figs. 60.* London: Ray Society. 1915.

the Ray Society in 1869. The older work has become naturally very incomplete, for during the last 50 years there has been an enormous increase in the knowledge of abnormal structures. The work will comprise two volumes, the first one containing the fungi, the bryophytes, and the root, stem, and leaf of the vascular plants. The algae are not included because they exhibit too few abnormalities to make description worth while. The second volume will deal with the flower. This bringing together of the great mass of material in convenient form will be a boon to those interested in teratology.—J. M. C.

**Western wild flowers.**—MARGARET ARMSTRONG,[3] in collaboration with J. J. THORNBER, has written a handy and well illustrated volume under this title, which, although primarily intended for lovers of wild flowers, will be useful to botanists as well. The wild flowers of Washington, Oregon, California, Idaho, Utah, and Arizona are dealt with, but those found only in the Rocky Mountains are not included. The key to families is an excellent feature, and the usefulness of the volume would be much greater had it been extended to species. The collaboration of Professor THORNBER insures the accuracy of the text.—W. J. G. LAND.

## NOTES FOR STUDENTS

**Transpiration studies.**—The desirability of giving a quantitative turn to ecological description and classification, together with the recognition that the most useful of such classifications have been based upon the water relations, has led to efforts to measure the power of the plant (1) to absorb water from its surroundings, (2) to distribute this water within its body, and (3) to prevent the loss of water to its environment. To study the third feature of the water relation some means of measuring the resistance offered by leaves and other parts of plants to water loss, or, stated in other words, of measuring the relative transpiring power of plants, has been needed. A further requirement of such a system is that it shall be readily applicable to plants growing in open soil. In seeking to meet this need LIVINGSTON[4] has modified the cobalt paper method of STAHL, and adapted it to compare the transpiring power of a leaf with evaporation from a standard surface, namely, that of saturated blotting paper shown by RENNER to evaporate water at the same rate as an equal area of free water surface. In a series of experiments he has shown that this new method is probably the most satisfactory known for comparing the same plant at different times, or for comparing different plants, in regard to the transpiring power of their surfaces. The ratio of the time required for color change of the standardized cobalt chloride paper exposed over the standard surface, to the

[3] ARMSTRONG, MARGARET, Field book of western wild flowers. 16mo. pp. xx+396. *figs. 548.* New York: Putnam. 1915.

[4] LIVINGSTON, B. E., The resistance offered by leaves to transpirational water loss. Plant World **16**:1–35. 1913.

corresponding time required for the same change when the paper is applied to the plant surface, he has termed the "index of transpiring power."

BAKKE,[5] in making use of this method, has shown that the experimental error incurred in determining the time of color change is not large, and further that it may be possible so to standardize the hygrometric paper that the constant use of the standard surface may be dispensed with by making a correction of a given time coefficient according to air temperature. In his own experiments, however, he continues to use the standard surface. Testing the leaves of 43 different species growing under irrigated conditions at the University of Arizona, indices were obtained ranging from 0.9288 for *Dahlia variabilis*, 0.8473 for *Verbena hybrida*, and 0.7893 for *Medicago sativa*, to 0.2258 for *Olea europea*, 0.1676 for *Nerium oleander*, 0.0603 for *Chenopodium incanum*, and 0.0025 for *Atriplex elegans*. These data would seem to afford a most satisfactory basis for ecological classification, and he makes the tentative proposition of including under mesophytes plants with diurnal foliar indices of transpiring power above 0.70, and of terming xerophytes all with indices below 0.30, with the possibility of an intermediate critical point at the index 0.50; the desirability and designation of the groups thus formed to be determined by further study. BAKKE also shows that the method may well be applied to the determination of the daily march of foliar transpiring power, and gives some data upon the relation of position upon the plant and age of leaves to their transpiring power, making his paper a good example of the use of this new technique in its possible application to various problems.

More recently, in studying the vegetation of the Santa Catalina Mountains, SHREVE[6] has measured the transpiring power of some 20 species and has found that (1) while the indices of the transpiring power are similar within various groups of life forms, they are not so to the extent that they may be predicted from an examination of the foliage of the plant; (2) the indicas ere higher in plants which grow in flood plains with good moisture supply than in individuals of the same species upon arid slopes; and (3) the transpiring power of a given species is not unlike at different altitudes, but the maximum value for the day is reached at an earlier hour at lower than at higher elevations, while for some species at some 6000 feet, no check in the rate is manifested, and the maximum transpiring power and maximum evaporation are simultaneous.

Some of these results were to be expected from the former results of Mrs. SHREVE,[7] obtained in a very exact study of the actual amount of water lost by the desert shrub *Parkinsonia microphylla*, using both potted plants and

[5] BAKKE, A. L., Studies on the transpiring power of plants as indicated by the method of standardized hygrometric paper. Jour. Ecology 2:145–173. 1914.

[6] SHREVE, F., The transpiring power of plants as influenced by differences of altitude and habitat. Science 43:363. 1916.

[7] SHREVE, EDITH B., The daily march of transpiration in a desert perennial. Carnegie Inst. Wash. Publ. no. 194. pp. 64. *figs.* 27. 1914.

branches on larger individuals growing in the open passed into a closed chamber under a bell glass, where the amount of water given off by the plant was found from the gain in weight of calcium chloride exposed within the chamber. Her method of work, as described, seems to provide against any vitiating errors, and clearly demonstrates in this shrub, both when leafless and in leaf, a distinct drop and subsequent rise in actual and relative transpiration (transpiration divided by evaporation) in the morning before the time of maximum evaporation for the day. The maxima for relative transpiration for potted plants were found to vary directly with the soil moisture, and some evidence was obtained that the same variation exists in plants growing naturally in the desert region about Tucson, Arizona. It was also found that *Parkinsonia* plants in sunlight exhibit hourly changes in the relative transpiration rate, in the amount of opening of stomata, in water content of leaves and twigs, and in leaf temperature, and that these have evident interrelations which are held to be governed by the ratio of the demand to the available supply of water.

The transpiration absorption water balance in this woody perennial, as it grows at Tucson, seems to be adjusted with the coming on of the summer drought conditions by (1) the leaflets beginning to close earlier each day, until finally they remain open only for a few minutes at dawn and twilight; (2) the transpiration amount being lessened with the drying out of the soil; (3) the leaflets and later the rachis dropping; and (4) the twigs and small branches beginning to die. In addition to these seasonal changes, there is a daily closing of leaflets and a lessening of actual transpiration rate, while the evaporating power of the air is still increasing. This decrease is accompanied by a closure of stomata, a lowered water content of leaves and twigs, and a slight rise in leaf temperature. The drop is followed by a rise, which, however, does not equal the former maximum. Mrs. SHREVE's investigation of *Parkinsonia* may serve as a model for the study in detail of the transpirational behavior of other similar and dissimilar plants in the accumulation of data necessary for the understanding of the relationship of vegetation to atmospheric and soil moisture. In attempting such studies, the investigators will do well to note her conclusion that relative transpiration rates were found to differ according to the previous environment of the plant, and hence that conclusions regarding the actual transpiration of plants *in situ* cannot be drawn from the measurement of losses from potted plants, but may be learned better from the measurement from small branches of the plant grown in its natural environment.

Among other recent contributions to our knowledge of transpiration is a study by GIDDINGS[8] of some excised leaves of *Silphium laciniatum*, where in a comparatively few experiments a comparison between rates of evaporation and transpiration showed that here also a check in the latter process occurred 1–3 hours before the daily maximum rate of evaporation was reached,

[8] GIDDINGS, L. A., Transpiration of *Silphium laciniatum*. Plant World **17**:309–328. 1914.

somewhere between 1:00 and 3:00 P.M., showing the influence of internal factors upon transpiration. The rate of evaporation was determined by Piche atmometers and transpiration loss by weighing closed bottles of water in which the excised leaves were inserted. Leaves taken from the same plant at heights of 13, 47, 71, and 100 cm. showed relative transpirational losses per unit area of 100, 114, 103, and 86, or a somewhat smaller loss from the upper leaves than from the lower ones placed under the same conditions.

BURNS[9] has compared the transpiration of *Pinus Strobus* seedlings grown in nursery beds unshaded, half shaded, and full shaded, with the evaporation from black and white atmometers, and has found a closer relation between the transpirational losses and those from the black atmometer. The relative transpiration was here for the unshaded, half shaded, and full shaded plants respectively 0.0633, 0.0346, and 0.0088, from which he calculated the amount of water transpired to be proportionately 21, 8, and 1 parts. A further comparison showed the average green weight of the unshaded, half shaded, and full shaded plants to be respectively 0.304, 0.166, and 0.090 gm.; while the dry weight was 0.063, 0.034, and 0.010 gm.; that is, the dry weight of the shadeless plants was 6 times that of the full shaded, and twice that of the half shaded plants. On the other hand, the nitrogen content in percentage of dry weight was respectively 2.18, 2.70, and 6.89, or nearly 3 times as much in the full shaded plants as in either of the others, showing that a large amount of transpiration is not to be related to the absorption of ash constituents. BURNS concludes that his experiment indicates that differences in size and chemical composition of these white pine seedlings must be sought along the line of photosynthesis and assimilation, rather than through absorption and transpiration.—GEO. D. FULLER.

**Taxonomic notes.**—COTTON[10] has described collections of cryptogams made by Mrs. ELINOR VALLENTIN, in 1909–1911, on the western islands of the Falklands. An interesting account of the phytogeography of the region is followed by systematic lists of marine algae (138 spp.), freshwater algae (54 spp.), lichens (95 spp.), and fungi (36 spp.). The representation of the four groups of algae is as follows: Cyanophyceae, 4 spp.; Chlorophyceae, 26 spp. (one new); Phaeophyceae, 39 spp.; Rhodophyceae, 69 spp. (one new). The list of fungi includes descriptions of 6 new species.

FERNALD and WEATHERBY[11] have investigated the perplexing genus *Puccinella*, a group of species placed by some in *Glyceria* and by others in *Fes-*

---

[9] BURNS, G. P., The relative transpiration of white pine seedlings. Plant World **18**:1–6. 1915.

[10] COTTON, A. D., Cryptogams from the Falkland Islands collected by Mrs. VALLENTIN. Jour. Linn. Soc. Bot. **43**:137–231. *pls. 4–10*. 1915.

[11] FERNALD, M. L., and WEATHERBY, C. A., The genus *Puccinellia* in Eastern North America. Rhodora **18**:1–28. *pls. 114–117*. 1916.

*tuca*. They distinguish 11 species from Eastern North America, including 4 new species, 4 new combinations, and a new variety. The full synonymy and extensive citations of exsiccatae should make the recognition of the species clear.

FOERSTE[12] has described a new genus (*Dictyophlois*) of rhizophores, related to those of *Stigmaria ficoides*, from the Subcarboniferous of western Kentucky.

HALL,[13] in continuing his studies of Californian plants, has described new species in *Brodiaea*, *Cymopterus*, *Pentachaeta*, *Haplopappus*, *Aster*, *Erigeron*, and *Arnica*.

HAYATA[14] has concluded that *Viscum japonicum* Thunb. is not congeneric with the other species of *Viscum*, and has made it the type species of a new genus, *Pseudixus*.

KOIDZUMI,[15] in presenting a fascicle of new or little known plants of Japan, has described new species in *Abelia*, *Salix* (2 spp.), and *Saussurea*.

In a "commemoration number" of the *Botanical Magazine* of Tokyo,[16] dedicated to Professor J. MATSUMURA on the occasion of the twenty-fifth anniversary of his professorship, the following taxonomic contributions appear: V. F. BROTHERUS and SHŪTAI OKAMURA describe a new genus (*Ishibaea*) of mosses belonging to the Brachytheciaceae; TAKENOSHIN NAKAI publishes a synopsis of the Korean species of *Saussurea*, including 24 species, 5 of which are described as new; YŪSHUN KUDŌ publishes a synopsis of the species of *Cacalia* in Northern Japan, recognizing 11 species, 2 of which are described as new; YOSHITADA YABE discusses some new or little known plants from Northern China, describing new species in *Deschampsia*, *Listera*, and *Clematis;* TOMITARO MIKINO describes 2 new genera, namely *Matsumurella* and *Ajugoides*, both of the Labiates (Stachydeae).

OSTENFELD[17] has described a new species of *Ruppia* (*R. anomala*) from Porto Rico, which differs from *R. maritima* and the other species of the genus in the development of the stipe of the fruit. In other species each sessile pistil, after fertilization, develops as a stipitate fruit; while in *R. anomala*

[12] FOERSTE, AUG. F., *Dictyophlois reticulata*, gen. et sp. nov. Bull. Torr. Bot. Club **42**:675–677. *pl. 33*. 1915.

[13] HALL, H. M., New and noteworthy Californian plants. II. Univ. Calif. Publ. Bot. **6**:165–176. *pl. 20*. 1915.

[14] HAYATA, BUNZŌ, On *Pseudixus*, a new genus of Loranthaceae founded on the well known and widely distributed species *Viscum japonicum* Thunb. Bot. Mag. Tokyo **29**:31–34. 1915.

[15] KOIDZUMI, GENICHI, Decades plantarum novarum vel minus cognitarum. Bot. Mag. Tokyo **29**:309–315. 1915.

[16] Bot. Mag. Tokyo **29**:161–283. 1915.

[17] OSTENFELD, C. H., *Ruppia anomala*, sp. nov., an aberrant type of the Potamogetonaceae. Bull. Torr. Bot. Club **42**:659–662. *pl. 32*. 1915.

the stipes develop together as a common stipe, at the summit of which the drupelets "are placed in a starlike manner."

STANDLEY,[18] in continuing his studies of tropical American plants, under a variety of titles has described numerous new forms as follows: *Wercklea* and *Peltaea*, new genera of Malvaceae; new species in Cyperaceae (2), Amaranthaceae (18; 11 of which belong to *Iresine*), Allionaceae (3), Caesalpiniaceae (4), Mimosaceae (4), Fabaceae (6), Ebenaceae (5; 3 of which belong to *Diospyros*), and Rubiaceae (20); also new species in *Geranium* (2), *Malache* (4), *Waltheria*, *Styrax*, *Exea* (2), *Duggena*, *Arctophyllum* (3), and *Psychotria* (11).—J. M. C.

**Inheritance of awns and velvet chaff.**—Students of genetic problems in wheat have arrived at conflicting conclusions, owing, no doubt, to the existence of biotypes possessing diverse factorial constitutions with respect to the characters under consideration. The HOWARDS have shown[19] that the velvet chaff of wheat may be of two distinct kinds, characterized by different types of hairs. Each kind of hair is produced by a distinct Mendelian factor, and the two kinds are mingled on the glumes when both of these factors are present. Only in the absence of both velvet factors are the glumes glabrous. Selfing any hybrid in which both velvet factors are heterozygous produces a progeny consisting of 15 velvet chaff to 1 glabrous. This result has received further confirmation in a recent paper by the same authors,[20] which is devoted chiefly to the inheritance of awns. Most of the genetical studies which have been made with the latter characteristic have involved forms which are not completely awnless. The HOWARDS used, among others, completely awnless varieties, and demonstrated that two independent factors affect the extent and nature of the awning. One of these factors (*T*) produces short awns or "tips" only, which are developed most conspicuously in the distal portion of the spike, while the other (*B*) also produces short awns, which are distributed more uniformly over the spike. The combined action of both of these factors in the homozygous state is required to produce the fully bearded condition. With respect to both of these factors, the heterozygote is successfully distinguished from the homozygotes by a distinctly intermediate condition. Completely bearded wheats have the formula *TTBB*, and the completely beardless are *ttbb;* the complete ratio of forms produced in the $F_2$ of a cross between awned and awnless forms,

[18] STANDLEY, PAUL C., Studies of tropical American Phanerogams. No. 2. Contrib. U.S. Nat. Herb. **18**:87–142. 1916.

[19] HOWARD, A., and HOWARD, GABRIELLE L. C., On the inheritance of some characters in wheat. II. Mem. Dept. Agric. India **5**:no. 1. 1912.

[20] ———, On the inheritance of some characters in wheat. II. Mem. Dept. Agric. India **7**:273–285. 1915.

therefore, is 1:4:2:2:1:2:1:2:1. The analysis was carried out on a commendably large scale and gave the following approach to expectation:

| | *BBTT* | *BbTt* | *BbTT* | *BBTt* | *BBtt* | *Bbtt* | *bbTT* | *bbTt* | *bbtt* |
|---|---|---|---|---|---|---|---|---|---|
| Observed..... | 16 | 54 | 40 | 33 | 15 | 22 | 13 | 24 | 13 |
| Expected..... | 15.4 | 61.6 | 30.8 | 30.8 | 15.4 | 30.8 | 15.4 | 30.8 | 15.4 |

It is clear that the results of this analysis will account for the discrepancies in the results of other investigators, since the short awned individuals may be classed on one basis with the awned, or on another basis with the awnless, and would naturally be classed either with the awnless, or as a distinct intermediate class, if a strictly awnless wheat had not been used in the cross.—GEO. H. SHULL.

**"Amphiclinous" hybrids.**—By this term DE VRIES[21] designates those $F_1$ hybrid progenies in which a portion of the individuals resemble the one parent, and the remainder resemble the other parent, a type of behavior which is not uncommon among crosses in the species of *Oenothera*. He describes such a cross between *O. Lamarckiana* and *O. Lamarckiana* mut. *nanella*. The percentage of *nanella* among the $F_1$ offspring of this cross can be modified by the conditions under which the mother plant is grown, from nearly 0 per cent to nearly 100 per cent. When the *Lamarckiana* mother was grown as an annual, the average percentage of *nanella* was 22; and when the *Lamarckiana* was grown as a biennial, the average number of *nanella* among the offspring reached 65 per cent. Corresponding with this result there is also a much higher percentage of *nanella* from capsules developed early in the season, when the mother is in most vigorous condition, than from capsules produced later in the season when vegetative vigor is declining. For example, on 3 different biennial *Lamarckiana* plants used in these extensive crosses, capsules developing July 12–23 yielded 73–88 per cent of *nanella*, those produced between July 24 and August 4 yielded 61–67 per cent *nanella*, and between August 5 and 16 the capsules produced 48–57 per cent *nanella*.

Another experiment showed that the time of transplanting has a marked influence on the percentage of *nanella* offspring, those reset on April 15 yielding 50 per cent, while plants of the same culture set out on May 15 produced only 29 per cent *nanella*. In this case the *Lamarckiana* mothers were grown as annuals. Further experiments showed that keeping the plants well watered also resulted in an increase in the percentage of *nanella* plants among the $F_1$ progeny.—GEO. H. SHULL.

[21] DE VRIES, H., Über amphikline Bastarde. Ber. Deutsch. Bot. Gesells. **33**:461–468. 1915.

**Chromosomes of Vicia.**—SAKAMURA[22] has found in the nuclei of the root tip of *Vicia Faba* during metaphase 12 already split chromosomes, 2 of which are considerably larger ("M-Chromosomen") and constantly showing middle and end constrictions ("m und e-Einschnürung"). In heterotypic mitosis these same constrictions are present in the one large bivalent ("M-Geminus"), which is believed to be composed of the two M-chromosomes. The fibers are attached at the end of the short chromosomes; but to the M-chromosomes and M-bivalent they are fastened at the middle, causing them to assume a V-shape when traveling to the poles. As a result, there are evident 14 arms in somatic anaphase, this feature probably being the cause of the 14-chromosome count; while in heterotypic mitosis, due to the splitting of each of the daughter chromosomes, there are 5 V's and one double V. The chief theory accounting for the origin of the "Einschnürung" is that the M-chromosomes at first are without constrictions, and then under certain conditions constrictions arise. This mechanism is shown to be due to an uneven separation of the chromosomes and to the strain of the fibers above this point, causing a stretching of the chromatin, so that when they do dissociate completely there is this apparent constriction. Before the m and e-constrictions could become hereditary characters they must first have occurred in heterotypic anaphase. While the investigation strengthens the individuality theory of the chromosomes, it throws little light upon the cause of the closely related species and varieties, two points that the author has attempted to prove.—MILDRED NOTHNAGEL.

**Vegetative vigor and reproduction.**—PIETERS[23] has made an interesting contribution to our knowledge of the structural responses of plants to varying chemical and physical conditions. The work of KLEBS, indicating that the appearance of reproductive cells is a response to diminishing vegetative activity, and that structures in general represent expressions of the potentialities of an organism, called out by the prevailing conditions for metabolism, has set in train investigations which should be multiplied. PIETERS used two species of *Saprolegnia* and two of *Achlya* in his investigations, and a summary of his results is as follows. There is no necessary relation between vegetative growth and sexual reproduction when the available food exceeds the minimum concentration necessary for the species. This minimum concentration of food necessary varies with the species, but in general is in the neighborhood of 0.1 per cent peptone for the production of both sporangia and oogonia. While growing vegetatively, a mycelium may develop tendencies that may affect the number and character of the reproductive organs produced subsequently under different conditions. Of the carbohydrates used, maltose and levulose are especially useful for vegetative growth, and the latter is particularly effect-

[22] SAKAMURA, TETSU, Über die Einschnürung der Chromosomen bei *Vicia Faba* L. Bot. Mag. (Tokyo) **29**:287–300. *pl. 13. figs. 12.* 1915.

[23] PIETERS, A. J., The relation between vegetative vigor and reproduction in some Saprolegniaceae. Amer. Jour. Bot. **2**:529–576. 1915.

ive in the production of oogonia. Sucrose is probably not used by species of *Saprolegnia* or *Achlya*. Phosphates in the culture solution tend to increase the reproductive capacity of the fungus.—J. M. C.

**Life forms of New York vegetation.**—RAUNKIAER has devised a method of classifying plants according to the way in which they pass the unfavorable season of the year, and by means of a numerical arrangement of these forms, known as a "biological spectrum," the flora of one region may be compared with that of the world as a whole. This journal has commented favorably upon these methods,[24] but they have been neglected by American workers as a whole. It is therefore pleasing to see them applied by TAYLOR[25] to the flora of New York. From the very nature of such investigations, the results will be more significant and valuable as a larger number of similar studies are made. Compared with the normal spectrum, the New York flora is higher in percentages of aquatics, geophytes, and hemicryptophytes, and somewhat lower in percentages of chamaephytes and phanerophytes. No other area to which this method of analysis has been applied has shown such an abundance of deep-rooted perennials of the bulb and rootstock type, here termed geophytes. This is to be correlated with and is partly explained by the large proportion of monocotyledons in the portion of the pine barrens included in the area studied. TAYLOR points out that were it possible to base the spectra upon a census of individuals rather than one of species, different and probably more significant comparisons would result.—GEO. D. FULLER.

**Disease resistance.**—JONES and GILMAN[26] have published a very suggestive bulletin upon the control of the cabbage disease known as "yellows," caused by the soil fungus *Fusarium conglutinans*. It seems that on badly infected or cabbage-sick soil the loss ordinarily ranges from 50 to 95 per cent. Experimental work through five summers seems to justify the conclusion that no method of soil, seed, or crop treatment offers any hope for the control of the disease. On the other hand, the development of disease-resistant varieties by selection has given such promising results that "full reliance can be placed in it as a feasible method for the practical control of this malady." Control of various commercial varieties of cabbage showed that there are marked differences in susceptibility among them, and advantage is taken of this fact to discover a *Fusarium*-resistant strain. The method employed has been based on the observation that even in the worst diseased fields in the autumn there are occasional sound heads, and these have been selected for pedigree culture.

[24] BOT. GAZ. **44**:303. 1907; **51**:309–310. 1911.

[25] TAYLOR, NORMAN, The growth forms of the flora of New York and vicinity. Amer. Jour. Bot. **2**:23–31. 1915.

[26] JONES, L. R., and GILMAN, J. C., The control of cabbage yellows through disease resistance. Agric. Exp. Sta. Univ. Wisconsin Bull. 38. pp. 70. *figs.* 23. 1915.

The results of this work have been so convincing that the cultivation of disease-resistant strains of our crop plants promises to be the final method of eliminating disease.—J. M. C.

**Ascospore expulsion of Endothia.**—HEALD and STUDHALTER[27] have published the results of an investigation of the chestnut blight fungus, which uncovers a very interesting situation. There is a remarkably prolonged perithecial activity, due, partly at least, to three important features in the development of the fungus. The asci mature successively through quite an extended period, the perithecia mature successively in a given stroma, and the stromata mature successively throughout the season. The practical result is that ascospores are available for expulsion at any time when the conditions favor. Expulsion "begins in the spring with the first warm rains, and increases to a maximum of activity as conditions become more favorable, to be followed by a decline in the fall when lower temperatures prevail, and ceases entirely during the cooler portions of the year."—J. M. C.

**Carpophores of pore fungi.**—ZELLER[28] has studied the development of the carpophores of *Ceriomyces Zelleri*, one of the pore fungi. He discovers that in this development there is a homogenous mass of tissue which is differentiated simultaneously into pileus and stipe by a cleavage plane which gives rise to an annular furrow, and that the hymenium, which is exogenous in origin, is formed in the roof of a furrow. This form proves to be gymnocarpic, since there is no marginal veil.—J. M. C.

**Morphology of Agaricus.**—ATKINSON[29] has described in great detail the development of *Agaricus Rodmani*, a species described by PECK in 1885. The four features which he considers are (1) the duplex character of the annulus, (2) the origin of the hymenophore fundament, (3) the differentiation of parts in the primordial ground tissue, and (4) the origin and development of the lamellae. The paper must be referred to for the numerous details involved.—J. M. C.

**New species of rust.**—In working over cultures of rusts in connection with their presentation in the *North American Flora*, ARTHUR and FROMME[30] have discovered and described 7 new species in *Uromyces* (2), *Puccinia* (4), and *Uredo*.—J. M. C.

---

[27] HEALD, F. D., and STUDHALTER, R. A., Seasonal duration of ascospore expulsion of *Endothia parasitica*. Amer. Jour. Bot. **2**:429–448. *figs. 6.* 1915.

[28] ZELLER, SANFORD M., The development of the carpophores of *Ceriomyces Zelleri*. Mycologia **6**:235–239. *pls. 140, 141. figs. 12.* 1914.

[29] ATKINSON, GEO. F., Morphology and development of *Agaricus Rodmani*. Proc. Amer. Phil. Soc. **54**:309–343. *pls. 7–13.* 1915.

[30] ARTHUR, J. C., and FROMME, F. D., New species of grass rusts. Torreya **15**: 260–265. 1915.

# GENERAL INDEX

Classified entries will be found under Contributors and Reviewers. New names and names of new genera, species, and varieties are printed in **bold face** type; synonyms in *italic*.


## A

Abdominea 262
Abscission in Mirabilis jalapa 213
Acacia 261
Acalypha 173
Actaea alba 193, 199; arguta 202; arguta alabastrina 202; arguta eburnea 202; arguta **pauciflora** 202; asplenifolia 204; caudata 204; neglecta 201; rubra 193, 199; rubra dissecta 199; rubra **gigantea** 201; viridiflora 203; viridiflora **Clementiorum** 203
Adams, J. 131
Adamson, R. S., work of 84
Adiantum 261
Aegiphila fasciculata 385
Affourtit, M. F. A., work of 176
Agaricus, morphology of 540
Aistopetalum 172
Ajugoides 535
Alcohol oxidation 173
Allard, H. A., work of 83
Allium tricoccum, reduction division in 453
Allocarya Cusickii **jucunda** 36; Scouleri **hirta** 36
American trees 344
Ames, O., work of 77
Amino acids 347
Amsinckia **Menziesii** 36
Anderson, H. W., work of 449
Andres, H., work of 77
Andrews, F. M., work of 449
Angatia 262
Angiosperms, phylogenetic taxonomy of 85
Anthocyanins 349
Aphanelytrum 342; spikelet of 340
Apocynum 77
Apple, germination of pollen 132
Appleman, C. O. 265
Arber, Agnes, work of 174, 451
Arenaria **macra** 30
Argentina, grasses of 262
Armstrong, Margaret, "Western wild flowers" 531
Arnaud, G., work of 77
Arnica 535
Arthur, J. C., work of 540
Asclepiadaceae 261
Asclepias cryptoceras, pollination of 72
Ashby, S. F., work of 444
Aster 535
Atkinson, G. F. 89; work of 540
Atmometry and the porous cup 450
Australian vegetation 440
Awns and velvet chaff, inheritance of 536
Aytonia, morphology of a Mexican 48

## B

Bachmann, H., "Das Phytoplankton des Süsswassers" 170
Bacteria in frozen soil 507; separating from fungi 247
Bactericidal substances 86
Baker, E. G., work of 77
Bakke, A. L., work of 532
Balfour, I. W., work of 77
Bancroft, N., work of 450
Barbeyella 172
Bartlett, H. H., work of 77
Basilocula 78
Beattie, R. K., "Flora of the northwest coast" 348
Beccari, O., work of 77
Beer, R., work of 174
Beets, chemistry of diseased 173
Belosersky, N., work of 77
Benedict, H. M., work of 435
Benedict, R. C. 77
Bennett, A., work of 77
Bennettitales, new genus of 449
Béquinot, A., work of 77
Berry, E. W., work of 84
Besleria **congestiflora** 379; **trichostegia** 380; triflora **subcorymbosa** 380
Bessey, C. E., work of 85
**Besseyosphaera,** a new genus of Volvocaceae 253; **Powersi** 254
Betchea 172
Bicknell, E. P., work of 77
Bidens 261; amplissima 504; **Andrei** 495; anthriscoides 497; **attenuata** 495; cernua 503; chinensis 490; **chrysanthemifolia** 501; crithmifolia 500; frondosa 498; hirtella 501; humilis 500; laevis 504; **mirabilis** 496; nodiflora 498; pilosa 497
Biovularia 171

The results of this work have been so convincing that the cultivation of disease-resistant strains of our crop plants promises to be the final method of eliminating disease.—J. M. C.

**Ascospore expulsion of Endothia.**—HEALD and STUDHALTER[27] have published the results of an investigation of the chestnut blight fungus, which uncovers a very interesting situation. There is a remarkably prolonged perithecial activity, due, partly at least, to three important features in the development of the fungus. The asci mature successively through quite an extended period, the perithecia mature successively in a given stroma, and the stromata mature successively throughout the season. The practical result is that ascospores are available for expulsion at any time when the conditions favor. Expulsion "begins in the spring with the first warm rains, and increases to a maximum of activity as conditions become more favorable, to be followed by a decline in the fall when lower temperatures prevail, and ceases entirely during the cooler portions of the year."—J. M. C.

**Carpophores of pore fungi.**—ZELLER[28] has studied the development of the carpophores of *Ceriomyces Zelleri*, one of the pore fungi. He discovers that in this development there is a homogenous mass of tissue which is differentiated simultaneously into pileus and stipe by a cleavage plane which gives rise to an annular furrow, and that the hymenium, which is exogenous in origin, is formed in the roof of a furrow. This form proves to be gymnocarpic, since there is no marginal veil.—J. M. C.

**Morphology of Agaricus.**—ATKINSON[29] has described in great detail the development of *Agaricus Rodmani*, a species described by PECK in 1885. The four features which he considers are (1) the duplex character of the annulus, (2) the origin of the hymenophore fundament, (3) the differentiation of parts in the primordial ground tissue, and (4) the origin and development of the lamellae. The paper must be referred to for the numerous details involved.—J. M. C.

**New species of rust.**—In working over cultures of rusts in connection with their presentation in the *North American Flora*, ARTHUR and FROMME[30] have discovered and described 7 new species in *Uromyces* (2), *Puccinia* (4), and *Uredo*.—J. M. C.

---

[27] HEALD, F. D., and STUDHALTER, R. A., Seasonal duration of ascospore expulsion of *Endothia parasitica*. Amer. Jour. Bot. **2**:429–448. *figs. 6*. 1915.

[28] ZELLER, SANFORD M., The development of the carpophores of *Ceriomyces Zelleri*. Mycologia **6**:235–239. *pls. 140, 141. figs. 12*. 1914.

[29] ATKINSON, GEO. F., Morphology and development of *Agaricus Rodmani*. Proc. Amer. Phil. Soc. **54**:309–343. *pls. 7–13*. 1915.

[30] ARTHUR, J. C., and FROMME, F. D., New species of grass rusts. Torreya **15**: 260–265. 1915.

# GENERAL INDEX

Classified entries will be found under Contributors and Reviewers. New names and names of new genera, species, and varieties are printed in **bold face** type; synonyms in *italic*.


## A

Abdominea 262
Abscission in Mirabilis jalapa 213
Acacia 261
Acalypha 173
Actaea alba 193, 199; arguta 202; arguta alabastrina 202; arguta eburnea 202; arguta **pauciflora** 202; asplenifolia 204; caudata 204; neglecta 201; rubra 193, 199; rubra dissecta 199; rubra **gigantea** 201; viridiflora 203; viridiflora **Clementiorum** 203
Adams, J. 131
Adamson, R. S., work of 84
Adiantum 261
Aegiphila fasciculata 385
Affourtit, M. F. A., work of 176
Agaricus, morphology of 540
Aistopetalum 172
Ajugoides 535
Alcohol oxidation 173
Allard, H. A., work of 83
Allium tricoccum, reduction division in 453
Allocarya Cusickii **jucunda** 36; Scouleri **hirta** 36
American trees 344
Ames, O., work of 77
Amino acids 347
Amsinckia **Menziesii** 36
Anderson, H. W., work of 449
Andres, H., work of 77
Andrews, F. M., work of 449
Angatia 262
Angiosperms, phylogenetic taxonomy of 85
Anthocyanins 349
Aphanelytrum 342; spikelet of 340
Apocynum 77
Apple, germination of pollen 132
Appleman, C. O. 265
Arber, Agnes, work of 174, 451
Arenaria **macra** 30
Argentina, grasses of 262
Armstrong, Margaret, "Western wild flowers" 531
Arnaud, G., work of 77
Arnica 535
Arthur, J. C., work of 540
Asclepiadaceae 261
Asclepias cryptoceras, pollination of 72
Ashby, S. F., work of 444
Aster 535
Atkinson, G. F. 89; work of 540
Atmometry and the porous cup 450
Australian vegetation 440
Awns and velvet chaff, inheritance of 536
Aytonia, morphology of a Mexican 48

## B

Bachmann, H., "Das Phytoplankton des Süsswassers" 170
Bacteria in frozen soil 507; separating from fungi 247
Bactericidal substances 86
Baker, E. G., work of 77
Bakke, A. L., work of 532
Balfour, I. W., work of 77
Bancroft, N., work of 450
Barbeyella 172
Bartlett, H. H., work of 77
Basilocula 78
Beattie, R. K., "Flora of the northwest coast" 348
Beccari, O., work of 77
Beer, R., work of 174
Beets, chemistry of diseased 173
Belosersky, N., work of 77
Benedict, H. M., work of 435
Benedict, R. C. 77
Bennett, A., work of 77
Bennettitales, new genus of 449
Béquinot, A., work of 77
Berry, E. W., work of 84
Besleria **congestiflora** 379; **trichostegia** 380; triflora **subcorymbosa** 380
Bessey, C. E., work of 85
**Besseyosphaera,** a new genus of Volvocaceae 253; **Powersi** 254
Betchea 172
Bicknell, E. P., work of 77
Bidens 261; amplissima 504; **Andrei** 495; anthriscoides 497; **attenuata** 495; cernua 503; chinensis 499; **chrysanthemifolia** 501; crithmifolia 500; frondosa 498; hirtella 501; humilis 500; laevis 504; **mirabilis** 496; nodiflora 498; pilosa 497
Biovularia 171

Birbal, S., work of 81
Bitter, G., work of 78
Black, J. W., work of 78
Blake, S. F., work of 78, 447
Blakeslee, A. F., work of 264
Bodnár, J., work of 173
Boedeker, F., work of 78
Bolton, K., work of 349
Bolus, L., work of 78
Bonati, G., work of 78
Boodle, L. A., work of 82
Borassodendron 77
Borgesen, F., work of 78
Botryochora 262
Botrytis cinerea 80
Bottomley, W. B., work of 263
Bovie, W. T. 1
Bower, F. O., work of 174
Bremiella 263
Brickellia 447
Brierley, W. B., work of 175
Brieya 263
Briggs, L. J., work of 175
Briquet, J., work of 78
Britton, N. L., work of 78
Brodiaea 535
Brotherus, V. F., work of 535
Brown, Lola B., work of 452
Brown, N. E., work of 78
Brown, W., work of 80
Brown, W. H., work of 87, 264
Brunnthaler, J., work of 170
Bubák, F., work of 78
Buergersiochloa 172
Burns, G. P., work of 534
Burt, E. A., work of 452
Bush, B. F., work of 78
Butler, E. J., work of 78

## C

Cacalia 535
Campbell, D. H., work of 447
Carboniferous plants 88
Cardamine cordifolia **Lyallii** 31
Cardot, J., work of 78
Carex 172, species of 452
Carnegieodoxa 260
Carpophores of pore fungi 540
Castagnella 77
Castilleja angustifolia **subcinerea** 45; confusa 44; confusa **pubens** 45; miniata **crispula** 45; pilosa **inverta** 44
Cecidiology 438
Celastrus **vulcanicolus** 373
Central America, new plants from 373
Centrantheropsis 78
Cephaelis tetragona 376
Cercospora 447
Cereus 262
Ceylon, endemic flora of 82
Chamaesyce 173
Chamberlain, C. J. 340, 353, 442; "Methods in plant histology" 347
Chase, Agnes 340
Cheiropleuria 174
Child, C. M. 435; "Senescence and rejuvenescence" 164
Chloroform as a paraffin solvent 251
Chodat, R., work of 78
Christensen, C., work of 78
Chromatophores, amoeboid movements of 85
Chromosomes of Vicia 538
Chrysactinia 447
Cladophora in deep water 87
Clarkia 31
Clintonia borealis 181; umbellulata 181
Coal, books on 258
Cobb, N. A., work of 430
Cochlospermum 260
Cockayne, L., work of 446
Coleman, D. A. 247
Colloid chemistry, texts on 345
Collomia 34
Columnea dictyophylla 385
Conceptacle, development of in Fucus 231
Coniothyrium 447
Contributors: Adams, J. 131; Appleman, C. O. 265; Atkinson, G. F. 89; Bovie, W. T. 1; Chamberlain, C. J. 340, 353, 442; Chase, Agnes 340; Child, C. M. 435; Coleman, D. A. 247; Cook, M. T. 67, 440, 444; Coulter, J. M. 81, 82, 85, 86, 87, 88, 170, 174, 175, 176, 263, 264, 346, 348, 349, 352, 443, 447, 448, 449, 452, 530, 534, 538, 539, 540; Cowles, H. C. 83, 84, 85, 170; Crocker, W. 345, 347, 352; Denny, F. E. 445; Fuller, G. D. 175, 344, 440, 445, 446, 450, 452, 531, 539; Gates, F. C. 399; Gates, R. R. 177; Greenman, J. M. 77, 171, 260; Harder, E. C. 507; Hasselbring, H. 79, 173; Heatley, Margaret 425; Hill, J. B. 255; Jeffrey, E. C. 75, 84, 88, 258, 450, 528; Kirkwood, J. E. 256; Kopeloff, N. 247; Land, W. J. G. 253, 347, 348, 447, 448, 451, 531; Lincoln, Mattie 408; Lint, H. C. 247; Lloyd, F. E. 213; Long, W. H. 417; McCormick, Florence A. 388; Macbride, J. F. 30; Mathews, A. P. 164; Merriman, Mabel L. 311; Michell, Margaret R. 325; Moore, B. 59; Mottier, D. M. 251; Nelson, A. 30; Nothnagel, Mildred 441, 453, 538; Osterhout, W. J. V. 148; Payson, E. 72; Pfeiffer, Norma E. 518; Phillips, T. G. 76; Reed, G. B. 430, 523; Rigg, G. B. 159, 295, 408; Roe, Mabel L. 231; Rose, J. N. 70; Scott, D. H. 434; Shaw, C. H. 477; Shaw, W. R. 253;

Sherff, E. E. 495; Shull, G. H. 536; Smith, J. D. 373; Starr, Anna M. 48; Trumbull, H. L. 408
Cook, M. T. 67, 440, 444
Cooley, J. S., work of 79
Copeland, E. B., work of 172
Coprinus, lamellae of 89
Copy, preparation of 337
Cordylanthus bicolor 45
Cotton, A. D., work of 534
Coulter, J. M. 81, 82, 85, 86, 87, 88, 170, 174, 175, 176, 263, 264, 346, 348, 349, 352, 443, 447, 448, 449, 452, 530, 534, 538, 539, 540
Coulter, S., work of 449
Cowiea 79
Cowles, H. C. 83, 84, 85, 170
Cox, H. J., work of 159
Crataegus 262
Cretaceous and eocene plants 84
Crocker, W. 345, 347, 352
Crotalaria 77
Cryptantha muricata 42; Torreyana **grandiflora** 43
Cryptopus 262
Culbertson, G., work of 449
Currant, germination of pollen 142
Cyclotheca 262
Cymbomonas 261
Cymopterus 535
Cyrtandraceae 171
Cystodendron 78

D

Dactylostalix 447
Damazio, L., work of 79
Davis, J. J., work of 175
Dean, Alletta F., work of 264
Dean, C. C., work of 449
De Candolle, C., work of 79
Decay and soil toxins 295
Dehydration of histological material 255
Delphinium **stachydeum** 31, Menziesii **fulvum** 30
Denny, F. E. 445
De Vries, H., work of 537
Diastema **micranthum** 377, platylomatum 381
Dictyophlois 535
Diels, L., work of 79
Discogyne 172
Disease resistance 539
Dodecatheon Jeffreyi 33; viviparum 33
Dunn, S. T., work of 79

E

Echeveria 261
Echinopsis 172
Ellisiodothis 262
Embryo sac of Richardia africana 325
Endoconidia 175
Endothia, ascopore expulsion of 540
Engler, A., work of 79
Englerophytum 171
Eocene and cretaceous plants 84
Episcia **acaulis** 378
Erigeron 535
Eriophorum 447
Espeletia 352
Eupatorium 447
Euphorbiaceae 172
Evans, A. W., work of 79
Exotrichum 262

F

Falklands, cryptogams of 534
Felt, E. P., work of 439
Fernald, M. L., work of 534
Ferns, Malayan 88
Filicales, phylogeny of 174
Fisher, M. L. 449
Fitting, H., work of 350
Foerste, A. F., work of 535
Frasera nitida **Cusickii** 33
Fromme, F. D., work of 540
Frozen soil, bacteria in 507
Fucus, development of conceptacle 231
Fuller, G. D. 175, 344, 440, 445, 446, 450, 531, 530; work of 452
Funastrum 261
Fungi, separating from protozoa and bacteria 247
Fyson, P. F., "Flora of the Nilgiri and Pulney hill-tops" 170

G

Gaillardia **crassifolia** 46
Gample, J. S., work of 79
Gates, F. C. 399
Gates, R. R. 177
Genetics, a new journal 530
Geomyces 262
Germination of pollen 131
Gesnera **Eggersii** 384; **Lehmannii** 384
Gibbs, L. S., work of 79
Giddings, L. A., work of 533
Gilgiochloa 79
Gilia 34; achilleifolia **Chamissonis** 34; floccosa **filifolia** 35; **mazama** 34; **tenella** 34
Gilibertia diplostemona 373
Gilletia 263
Gilman, J. C., work of 539
Ginkgo, pollen grains 81; seeds of 176
Giorgiella 263
Gloiophloea 261
Gnaphalium **Grayi** 46; **Ivesii** 46
Gnetum, morphology of 82; strobilus of 443

Goethalsia 261
Goff, E. S., "Plant culture" 530
Goodspeed, T. H., work of 86
Grass embryo 451
Greene, Edward Lee, biographical sketch 70; work of 171
Greenman, J. M. 77, 171, 260; work of 88
Griffithia 78
Guam, flora of 172
Gymnolomia 447
Gymnosperms, notes on 81
Gyranthera 261

## H

Hackel, E., work of 262
Hakonechloa 172
Hall, H. M., work of 535
Hamet, R., work of 171
Hamshaw, T. H., work of 81
Haplocalymma 447
Haplopappus 535
Harder, E. C. 507
Hardy, A. D., work of 441
Hasselbring, H. 79, 173
Hassler, E., work of 171
Hayata, B., work of 535
Heald, F. D., work of 540
Heatley, Margaret 425
Heimlich, L. M., work of 449
Heliotropium 447; curassavicum **xerophilum** 35
Herpotrichiella 260
Herter, W., work of 171
Hibiscadelphus 261
Hieracium **cineritium** 47
Hieronymus, G., work of 171
Hill, J. B., 255
Hill, T. G., "Essentials of illustration" 349
Hippeastrum 263
Höber, R., work of 340
Hoffmannia **nesiota** 374
Horkelia **Tweedyi** 31
Howard, A., work of 536
Howard, G. L. C., work of 536
Howe, M. A., work of 171
Hoyopsis 172
Huber, J., work of 171
Hue, A., work of 171
Humicola 262
Humirianthera 171
Hutchinson, J., work of 171
Hybridization and water requirement 175
Hybrids, amphiclinous 537
Hydrogen ion concentration 76

## I

Illustrations 349; preparation of 338
Impomoea Batatas, tuber of 388
India, flora of 170
Indiana Academy 449
Inga 171
Isertia Deamii **stenophylla** 374
Ishibaea 535
Isoetes, anatomy of 352; occidentalis **Piperi** 30
Isoloma **oblanceolatum** 383; **pycnosuzygium** 382; **vulcanicolum** 382

## J

Jeffrey, E. C. 75, 84, 88, 258, 450, 528, 539
Jones, L. R., work of 539
Jorgensen, I., work of 445

## K

Kaernbachia 172
Kahn, A. H., work of 78
Kania 172
Keysseria 172
Kindle, E. M., work of 87
Kingdonia 77
Kirkwood, J. E. 256
Kofoid, C. A., work of 171
Koidzumi, G., work of 535
Kopeloff, N. 247
Kränzlin, F., work of 171
Krause, K., work of 171
Kudō, Y., work of 447, 535
Kuhlman, J. G., work of 171
Küster, E., work of 85

## L

La Rivière, H. C. C., work of 176
Lamellae of Coprinus 89
Laminaria, permeability in 148
Land, W. J. G. 253, 347, 348, 447, 448, 451, 531
Lang, W. H., "Studies in the morphology of Isoetes" 352
Lappula arida **Cusickii** 41; cenchrusoides 38; cupulata 39; cupulata **foliosa** 40; diffusa 42; echinata 37; Fremontii 37; Redowskii occidentalis 38; Redowskii **patula** 39; subdecumbens 42; texana 40; texana **coronata** 41; texana **heterosperma** 41; texana **homosperma** 41
Larix, bisporangiate cones of 256
Lauterbach, C., work of 171
Lawson, A. A., work of 441
Leaf anatomy of Veronica 84
Leaves, age changes in 435; xerofotic movements in 399
Lemmermann, E., work of 170
Lepidium bonariense 262
Leptomassaria 260
Léveillé, H., work of 172
Lewis, I. M., work of 88
Liabum 447

Life forms of New York vegetation 539
Lignier, O., work of 176
Lincoln, Mattie 408
Lint, H. C. 247
Livingston, B. E., work of 450, 531
Lloyd, F. C. 213
Lobocolax 171
Loganberry, germination of pollen 141
Long, W. H. 417
Lophoschoenus 79
Ludwig, C. A., work of 449
Lunell, J., work of 172
Luzula 447
Lychniothyrsus 261
Lycopodium 171
Lythrum 260

## M

Macbride, J. F. 30; work of 447
Mackenzie, K. K., work of 172, 452
McCormick, Florence A. 338
Maianthemum canadense 189; dilatatum 189
Maiden, J. H., work of 440
Majanthemum **dilatatum** 30
Makino, T., work of 172, 447
Malayan ferns 88
Mallison, H., work of 349
Mamillaria 261
Manilaea 262
Marattiaceae, secretory tissues of 176
Marine algae in fresh water 452
Marsh, evaporation in 450
Marsonia 447
Martelli, U., work of 172
Martin, K., work of 349
Mathews, A. P. 164
Mathews, F. S., "Field book of American trees and shrubs" 344
Matsumurella 535
Meconella **linearis** 31
Medinilla 172
Meiotic divisions 441
Melastomaceae 172
Meliolina 262
Melliniella 79
Melochia 171
Melophia 447
Memecylon 172
Merrill, E. D., work of 172
Merriman, Mabel L. 311
Mesozoic plants 75
Metaporana 78
Meyer, R., work of 172
Meylan, C., work of 172
Michaelis, L., "Die Wasserstoffionenkonzentration" 76
Michell, Margaret R. 325
Microcyclella 262
Microseris nutans **macrolepis** 47
Microtechnique 448
Mieg, W., work of 349
Mikino, T., work of 535
Millspaugh, C. F., work of 172
Mimulus Langsdorfii **microphyllus** 44
Mirabilis jalapa, abscission in 213
Mitella 261
Mitosis, periodicity in 442
Miyage, K., work of 447
Miyake, I., work of 447
Mobius, M., "Mikroskopisches Praktikum" 348
Moeszia 78
Monilia cinerea 80
Moore, A. H., work of 173
Moore, B. 59
Moore, Emmeline, work of 451
Moore, S., work of 173
Mosaic disease of tobacco 83
Moss, a fossil 176
Mottier, D. M. 251
Mucors, sexual reactions of 264
Muhlenbergia **setiglumis** 30
Multinucleate cells 174
Muschleria 173
Myxomycetes of Wisconsin 264

## N

Nagai, I., work of 448
Nakai, T., work of 535
Neea **amplifolia** 386
Nelson, A. 30
Nematostoma 262
Neosabicea 262
Neosloetiopsis 79
New Guinea, flora of 176
New York vegetation, life forms of 539
New Zealand vegetation 446
Nicotiana, parthenogenesis in 86
Nicotiana **Torreyana** 43
Nieuwland, J. A., work of 260
Nolan, T. J., work of 349
Norlind, V., work of 260
North American flora 349
Nothnagel, Mildred 441, 453, 538; work of 449
Nuclear division of Spirogyra 311
Nylanderiella 171

## O

Odontoschizon 262
Okamura, S., work of 535
Onagra 77
O'Neal, C. E., work of 449
Ophioglossum vulgatum, prothallia of 518
Opocunonia 172
Oreocarya cilio-hirsuta 43; **salmonensis** 43
Ornamental plants, pathology of 67

Osborn, T. G. B., work of 441
Osmotic pressure 408
Ostenfeld, C. H., work of 535
Osterhout, W. J. V. 148
Ostermeyer, F., work of 260
Oswald, W., "Colloid chemistry" 345
Overholts, L. O., work of 452
Oxidase reagents, color changes in 430
Oxidases 523
Oxidation, alcohol 173; measurement of potential 523

## P

Pachylophus **psammophilus** 32
Pairs of species 177
Pandanaceae 172
Papua, flora of 172
Parasitic fungi of Wisconsin 175
Parasitism, phenomena of 79
Parlamium 79
Parmulina 262
Parthenogenesis in Nicotiana 86
Pascher, A., "Die Süsswasser-Flora" 170
Pathology of ornamental plants 67
Patouillard, N., work of 260
Payson, E. 72
Pear, germination of pollen 139
Pearson, H. H. W., work of 82, 443
Pectinella 78
Pedicularis contorta ctenophora 44
Pellaea 536
Pentachaeta 535
Perideridia 32; americana 33; **Bolanderi** 33; **californica** 33; **Parishii** 33; **Pringlei** 33; **simplex** 33
Perkins, J., work of 260
Permeability 445; decrease of by anesthetics 148
Peru, marine algae of 171
Perymenium 447
Petrak, F., work of 260
Pfeiffer, Norma E. 518
Phacelia **argentea** 34
Phaeodothiopsis 262
Phaeoschiffnerula 262
Philibertia 261
Philibertiella 78
Philippines, flora of 172; fungi of 262
Phillips, T. G. 76
Phloem, medullary 451
Phoebanthus 447
Phragmodothis 262
Phyllocactus 262
Phyllocrater 79
Physaliastrum 172
Physalis **porphyrophysa** 377
Phytomorula 117
Pickett, F. L., work of 449
Pieters, A. J., work of 538
Pilger, R., work of 260
Pillansia 78
Ping, C., work of 439
Pinus Laricio, concrescent leaves of 82
Pionocarpus 447
Pipel, F. J., work of 449
Piper, C. V., "Flora of the northwest coast" 348
Piricauda 78
Pittier, H., work of 261
Plankton studies 170
Plant culture, principles of 530
Plant pathology in tropics 444
Plectodiscella piri 263
Pleuropetalum **tucurriquense** 387
Polemoniella **antarcticum** 35; **Gayanum** 35
Pollen, germination of 131
Pollination of Asclepias cryptoceras 72
Polyclypeolum 262
Polygala 78, 260
Polypodium vulgare **hesperium** 30
Polyporaceae 452
Pore fungi, carpophores of 540
Potamogeton 451
Potonié, H., "Die rezenten Kaustobiolithe und ihre Lagerstaetten" 259
Prankerd, T. L., work of 174
Protozoa, separating from fungi 247
Psalidosperma 262
Pseudixus 535
Pseudoscinaia 261
Pteris 171
Puccinella 534
Puccinia 540
Pullea 172
Purpus, J. A., work of 261
Pycnoderma 262
Pyrenobotrys 262
Pyronema, development of 264

## Q

Quehl, L., work of 261

## R

Rachiopteris 450
Radlkofer, L., work of 261
Rafflesia and its host 87
Ramsey, G. B., work of 449
Ranunculus 171; abortivus 191; allegheniensis 191
Raspberry, germination of pollen 142
Ravenelia **annulata** 423; **morongiae** 418; **reticulatae** 421; **roemerianae** 418; **thornberiana** 420
Ravine, humidity of 445
Reduction divisions in Allium tricoccum 453
Reed, G. B. 430, 523
Rehmiodothis 262
Reproduction and vegetative vigor 538
Rest period in tubers of Solanum tuberosum 265

Reviews: Armstrong's "Western wild flowers" 531; Bachmann's "Das Phytoplankton des Süsswassers" 170; Beattie's "Flora of the northwest coast" 348; Chamberlain's "Methods in plant histology" 347; Child's "Senescence and rejuvenescence" 164; Fyson's "Flora of the Nilgiri and Pulney hill-tops" 170; Goff's "Plant culture" 530; Hill's "Essentials of illustration" 349; Mathews' "Field book of American trees and shrubs" 344; Michaelis' "Die Wasserstoffionenkonzentration" 76; Möbius' "Mikroskopisches Praktikum" 348; Oswald's "Colloid chemistry" 345; Pascher's "Die Süsswasser-Flora" 170; Piper's "Flora of the northwest coast" 348; Potonié's "Die rezenten Kaustobiolithe und ihre Lagerstaetten" 259; Stevenson's "Formation of coal beds" 258; Stopes' "Mesozoic plants" 75; Taylor's "Chemistry of colloids" 345; Thoday's "Botany" 346; Underhill's "Physiology of amino acids" 347; White's "The origin of coal" 259; Worsdell's "Plant teratology" 530
Rhamphogyne 173
Rhodohypoxis 70
Richardia africana, embryo sac of 325
Ricinophyllum **horridum** 45
Rigg, G. B. 159, 295, 408
Rizalia 262
Robinson, B. L., work of 447
Rock, J. F., work of 261
Roe, Mabel L. 231
Rolfe, R. A., work of 261
Root nodules 263
Rose, J. N. 70
Rosenbingea 78
Rosendahl, C. O., work of 261
Rubiaceae 262
Rudgea **thyrsiflora** 375
Ruppia 535
Rust, new species of 540

## S

Saccolaria 171
Safford, W. E., work of 261
Sakamura, T., work of 538
Salvia **Collinsii** 386
Sargent, Ethel, work of 451
Saunders, E. R., work of 441
Saussurea 535
Scenecio canus **celsus** 46; monograph of 88
Schaffner, J. H., work of 261
Schantz, H. L., work of 175
Schiller, J., work of 261
Schlechter, R., work of 261
Schmidleia 261
Schröder, B., work of 261
Schroederiella 261
Schulz, O. E., work of 261
Schumann rays, action on living organisms 1
Scinaia 261
Scleria 447
Scott, D. H. 434
Sears, P. B., work of 450
Seeds of Ginkgo 176
Selaginella 171
Selkirks, vegetation of 477
Senescence and rejuvenescence 164
Setchell, W. A., work of 251
Sex determination 87; influence of nutrition on organs 448
Shaw, C. H. 477
Shaw, W. R. 253
Sherff, E. E. 495
Shibataea 172
Shive, J. W., work of 450
Shreve, Edith B., work of 532
Shreve, F., work of 532
Shull, G. H. 536
Sidalcea 171
Sigmatochilus 79
Slosson, M., work of 261
Smith, G. M., work of 448
Smith, J. D. 373
Smith, J. J., work of 262
Smith, W. W., work of 77
Sohnreyia 261
Soil toxins and decay 295
Solanum 263; tuberosum, rest period in tubers of 265
Solms-Laubach, biographical sketch of 433
South America, new plants from 260
Species, pairs of 177
Spergularia **bracteata** 30
Sphagnum bogs, physical conditions in 159
Spiraea alba 205; tomentosa 205
Spirogyra, nuclear division of 311
Spirotheca 261
Spratt, Ethel R., work of 263
Stalagmites 262
Standley, P. C., "The genus Espeletia" 352; work of 536
Stangeria paradoxa 353
Stapf, O., work of 262
Starr, Anna M. 48
Stephanospora 260
Stevenson, J. J., "Formation of coal beds" 258
Stewart, A., work of 438
Stigmopsis 78
Stiles, W., work of 445
Stollaea 172
Stopes, Marie, "Mesozoic plants" 75; work of 88

Strawberry, germination of pollen 140
Streptopus amplexifolius 185; roseus 185; **streptopoides** 30
Stuckert, T., work of 262
Studhalter, R. A., work of 540
Succession from pine to oak 59
Surface tension 411
Sydow, H., work of 262
Sydow, P., work of 262

## T

Taylor, N., work of 539
Taylor, W. W., "Chemistry of colloids" 345
Technique 348
Tephrosticta 262
Teratology 530
Tetrault, P. A., work of 449
Texas, trees of 88
Text, preparation of 337
Theissen, F., work of 262
Theleophoraceae 452
Thellung, A., work of 262
Thiessen, R., "The origin of coal" 259
Thiessenula 262
Thoday, D., "Botany" 346
Thomas, H. H., work of 449
Thompson, M. T., work of 438
Tobacco, mosaic disease of 83
Tofieldia 447
Torrend, C., work of 262
Toxic solutions, physical properties of 408
Traaen, A. E., work of 262
Trabutiella 262
Transeau, E. N., work of 176
Transpiration studies 531
Travelbee, H. C., work of 449
Trees of Texas 88
Treubia, morphology of 447
Trichodothis 262
Trifolium **Kennedianum** 31
Trillium cernuum, life history of 425
Triplotaxis 171
Tropics, plant pathology in 444
Trumbull, H. L. 408

## U

Ule, E., work of 262
Ullrich, F. T., work of 445
Underhill, F. P., "Physiology of amino acids" 347
Urban, I., work of 262
Uredo 540
Uromyces 540
Utricularia 447

## V

Vanoverbergh, M., work of 172
Van Rosenburgh, Capt. C. R. W. K., work of 88
Verbesina 447
Veronica, leaf anatomy of 84
Verticilliodochium 78
Vicia, chromosomes of 538
Victoriella 261
Viguiera 447
Viola 171
Vittaria 77
Volutellopsis 263
Volvocaceae, a new genus of 253

## W

Wadsworth, J. T., work of 440
Wagner, R. J., work of 86
Weatherby, C. A., work of 534
Weatherwax, P., work of 449
Wedelia 171
Weingart, W., work of 262
Wercklea 536
Wernham, H. F., work of 262
West, C., work of 176
White, D., "The origin of coal" 259
Wildeman, E. de, work of 263
Williamsonia gigas, staminate strobilus of 81
Williamsoniella 449
Willis, J. C., work of 82
Willstätter, W., work of 349
Wilson, G. W., work of 263
Wilson, M., work of 87
Wisconsin, myxomycetes of 264
Wittmack, L., work of 263
Woolery, Ruth, work of 441
Worcesterianthus 172
Woronichin, N., work of 263
Worsdell, W. C., "Plant teratology" 530; work of 451
Wright, C. H., work of 263

## X

Xerofotic movements in leaves 399

## Y

Yabe, Y., work of 535

## Z

Zaleski, W., work of 174
Zeiller, C. R., sketch of 528
Zeller, S. M., work of 540
Zephyranthes 263
Zexmenia thysanocarpa 376
Zollinger, E. H., work of 349
Zygnemales 176